Morphology and Taxonomic Use of Ephemeroptera Eggs[1]

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ABSTRACT

Mayfly eggs possess 4 main morphological features which may be used for taxonomic purposes: chorionic sculpturing, polar cap(s), accessory attachment structures, and micropylar devices. A new and simple technique is described for observing these structures.

A detailed morphological description of the egg is presented, including terminology for the parts of the micropylar device.

The eggs were found useful for generic or specific determinations for the Heptageniidae, Leptophlebiidae, Caenidae, Ephemeridae, and Polymitarcidae; and of doubtful value for the Ephemerellidae, Tricorythidae, and Potamanthidae. Their value in taxonomy is not now assessible for the Siphlonuridae and Ametropodidae.

At the present time it is impossible or at least very difficult to determine most female mayflies to species when taken without males, and in many cases it is equally as difficult to identify them to genus. This difficulty develops from the lack of characters, especially genital differences as found in males. Likewise, specific identification of immatures is frequently difficult or impossible, because they have not yet been reared or otherwise associated with identified adults, or because reliable characters have not yet been found. Therefore, I undertook this study in an attempt to discover characters for separating and identifying immature and adult female Ephemeroptera from which eggs may be removed. The eggs possess morphological characters which are far more dependable than the body coloration of the adult. However, since closely related species often possess very similar or indistinguishable eggs, one should not necessarily conclude that 2 groups of specimens are of the same species if the eggs are identical. On the other hand, if the eggs are distinctly different they can serve to separate females of closely allied species. Distinct polymorphism has been noted within only 1 species, *Caenis simulans* McDunnough, and this situation may be a case of sibling species. The study of eggs will also aid in the association and identification of undescribed adults and immatures. The contribution of studies of eggs to insect taxonomy has been shown by

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the following, among others: Onsager and Mulkern (1963), Orthoptera; Ross and Horsfall (1965), Culicidae; Knight et al. (1965a, b), Plecoptera; Degrange (1960), Ephemeroptera; and Southwood (1956), Heteroptera.

Detailed studies of mayfly eggs began in Europe with Burmeister's (1848) discussion and illustration of the egg and embryo of *Ephoron virgo* (Olivier). He at first considered the polar cap to be a local thickening of the chorion, and later thought it might be the corpus luteum; he did not mention the micropyle. Leuckart (1855, p. 200–3, pl. x) described the polar cap of *E. virgo* as being a mass of spermatozoa attached to the micropylar apparatus (Fig. 72–75). Citing Swammerdam (1737), Leuckart (1855) supports his theory by the absence of this "mass of spermatozoa" on eggs in the ovaries; he also presents a direct comparison of what he saw (the polar cap) to spermatozoa. However, Grenacher (1868) and Palmen (1884) found the same structure on eggs taken from immature *Potamanthus* sp. Although classifying the caps with micropylar apparatuses, Grenacher did call them "polar caps"; Palmen correctly referred to their function of attachment. Grenacher felt that he discovered a simple porelike micropyle connected externally to a shallow depression, and sometimes bearing the internal micropylar canal. He found these at the poles of the egg, and unfortunately he observed that portion of the chorion which supports the cap. Grenacher noticed also some threads attached to the chorion and terminated by spherical knobs; he correctly surmised that these were attachment structures. Bengtsson (1913) studied the eggs of 28 Palearctic species, and believed that he found the micropyle on 3 of them: *Ephemerella lactata* Bengtsson, *Chitonophora aurivilii* Bengtsson, and *Caenis horaria* (L.). Like Grenacher, Bengtsson actually observed that portion of the chorion which supports the cap.

Morgan's (1913) discussion and illustration of 13 species of mayfly eggs was the first major morphological study published in North America. However, she did continue the use of the term "micropylar apparatus" for "polar cap." The only other major North American study was that of Smith (1935), who illustrated the eggs of 51 species, and discussed the eggs of 130 species. Unfortunately he frequently misinterpreted the chorionic sculpturing, thus negating many of his conclusions concerning the chorion. However, he did interpret quite accurately those accessory attachment structures which he found; he referred to polar caps correctly, but did not mention the micropyle. Aside from these studies, observations on mayfly eggs in North America have been minimal. Occasionally workers have had a passive interest in mayfly eggs, but they have never produced a study of more than 2 or 3 species, and none has observed the micropyles.

Degrange (1956, 1960) studied the European fauna and was the first to find and describe the micropyles on the eggs of mayflies. Previously all workers looked at the polar cap and polar areas in their search for the micropyle; Degrange found it to be lateral in position. Degrange (1956) first published a description of 4 types of micropyles on eggs of 24 species of mayflies and later (1960) published a paper on the reproduction of mayflies. A section of the latter was devoted to descriptions of eggs of 51 species and it illustrated eggs of 34 species. Degrange used fresh and hatched eggs whenever possible.

The present work is based mostly on a study of material from the Eastern United States and Canada. Therefore, my remarks that certain features of the eggs are a constant characteristic of the family or genus are drawn from, and are true for, the material reported on in this paper and that mentioned earlier.

TECHNIQUES

Standard resin mounts are unsatisfactory for studying the chorionic sculpturing of the eggs, because the contents are opaque and form a background of "bubbles" which conceals the surface details (Fig. 12, 30, 31, 61). Reflected light, rather than transmitted light, was tried without success. Because of this "contents" problem, most of the earlier workers experienced difficulties and included the egg contents on their drawings.

Many clearing techniques were tried, and when effective they rendered the eggs too fragile for handling and for transferring to a slide. A General Biological Supply House product, CMC-S, has proved to be the most efficient mounting medium. Since CMC-S contains a red stain and a clearing agent, eggs mounted in it will clear to a certain degree and be stained in the same process. However, CMC-S is a water-base mounting medium, making it necessary to ring the coverslip with asphalt or other suitable ringing compound.

It is possible to obtain fully developed eggs from final instar immatures, and I found that in many cases this was necessary. Since adult life of mayflies is so short, and given over entirely to mating and egg laying, there is no time in the adult life for egg maturation; therefore it is accomplished during the immature stages.

Adults are best preserved in 70% ETOH when collected, and immatures are best preserved in 95% ETOH when collected, and transferred to 70% ETOH a week later. Eggs removed from specimens preserved in 70% ETOH and collected within 5–10 years of slide mounting were usually clear enough for study within a week. Specimens remaining in preservative for a longer period (especially if in 95% ETOH) usually required 3–4 weeks for sufficient clearing; however, frequently the shape of the egg was distorted. A specimen collected in 1924 yielded eggs that were distorted, but they did clear well enough for observation of the chorion.

The female specimens were initially soaked in water for a few minutes to rinse off the preservative. The eggs were then removed from the abdomen into a water-filled cell on a spot plate, where they remained for 10–20 min before they were slide mounted. This waterbath cleanses the eggs of alcohol, which is

not miscible with CMC-S. *It is of utmost importance to keep the number of eggs per slide to a minimum.* Large numbers of eggs on a slide prevent the mounting medium from clearing the eggs quickly or effectively enough for observation and photography.

Where possible, 2 slides were made from the eggs of a single specimen. I retained 1 set of these slides, and the other set, together with the specimens used, remains in the Entomology Museum of Michigan State University.

For many species, duplicate slides were made from specimens collected in different localities, to determine variation in details. No significant variation in egg characters was found to occur between individuals of a given species, with the possible exception of *C. simulans* (as presently understood).

Because it is nearly impossible to interpret most details at lower magnifications, a magnification of 1000× or greater, on a phase-contrast microscope, is recommended. In this study, a phase microscope was used with magnifications of 125×, 500×, and 1250× (oil immersion) for examining the eggs. With few exceptions, magnifications of 400× and 1000× (oil immersion)were used for photography. When viewing and photographing details in relief (tangential view) ordinary bright-field lighting was superior to phase lighting. All photographs were made with an Exa IIa 35 mm camera, with Kodak Panatomic-X film.

ABBREVIATIONS USED IN FIGURES

ab = apical brush of micropylar canal (*Stenonema*)
al = adhesive layer
as = accessory attachment structure
dr = rim of raised disc
f = furrows (strands of reticulation)
l = length of mesh
m = micropyle
mc = micropylar canal
md = micropylar device
p = puncture
pc = polar cap
pr = pseudoreticulation (*Habrophlebiodes americana*)
r = ridges (strands of reticulation)
sg = sperm guide
sgh = sperm guide hood (*Stenonema*)
t = tubercle
ta = terminal appendage of micropylar canal (*Stenonema*)

MORPHOLOGY

The basic shape, or form, of the egg varies from ovoid to nearly rectangular, excluding the polar caps. However, the polar caps are described also as part of the form, since they do contribute to the general appearance of the egg.

Length and width dimensions of mayfly eggs have been given in past literature (Morgan 1913, Smith 1935, Degrange 1960), and most range from 150 to 200μ in length by 90–150μ in width. The eggs of larger mayflies (e.g., *Ephoron, Hexagenia*) are 250–300μ long by 150–200μ wide. Length and width dimensions are not given in this study, because it was found that the pressure of the coverslip caused measurements to be at least 50μ greater than those cited in the literature. Measurements made with eggs placed in a welled slide agreed with measurements given in the literature. With the use of slide mounts for the study of the eggs, it is apparent that length and width measurements would be too variable and inaccurate to include as morphological characters.

Mayfly eggs possess 4 main morphological features which may be used for taxonomic purposes: chorionic sculpturing, polar cap(s), accessory attachment structures, and micropylar devices. Chorionic sculpturing is often an excellent specific characteristic. Sculpturing may be tuberculate, peglike, netlike, rugose, punctate, or maculate. Tubercles are considered to be small bumps or protuberances which, at first glance, appear simply as maculations; peglike structures are longer, more definite projections than tubercles, and are considered to have an adhesive function. When the sculpturing is netlike, it is referred to as the reticulation. There are 2 types of reticulation, one formed by raised ridges (Fig. 67) and the other by depressed furrows (Fig. 47), which are collectively termed the strands. Therefore, the mesh, the areas between the strands, may be of either raised or depressed surfaces. Thus, when discussing a netlike sculpturing, a net, its fibers, and spaces will be considered to correspond respectively to the reticulation, its ridges or furrows (strands), and mesh. The size of the mesh of the reticulation has been found to be of value in discerning taxa. The mesh has been consistently measured across its greatest inside dimension (excluding the strands), and this measurement is given as the length of the mesh (Fig. 47). A large-mesh reticulation (Fig. 67) would be readily visible under lower magnifications (125×), whereas under the same magnification, a small-mesh reticulation (Fig. 31, 32, 63), if apparent at all, would be difficult to discern. Structural details of the chorion, such as tubercles and ridges, are discussed with chorionic sculpturing when it is uncertain whether they play a role in attachment; otherwise they are discussed with attachment structures.

To insure survival and aid dispersal, mayfly eggs must have a means of attachment to submerged objects and the substrate. This is especially important in lotic waters, wherein maximum dispersal is probably attained when some eggs adhere to submerged surfaces soon after deposition, while others move farther downstream. Attachment structures thus prevent most eggs from being washed downstream, as well as from being carried to an environment unsuitable for development. Lentic species have eggs that are equally equipped with attachment structures, and here the lake currents must serve to disperse the eggs away from the oviposition site and bring them in contact with submerged objects to which they adhere. Concerning the eggs of *Hexagenia limbata* (Serville) s. lat., Hunt (1953) stated:

"Laboratory experiments showed that in still water individual eggs sank at an average rate of 1 foot in 80 seconds, and small clumps of eggs settled 1 foot in about 60 seconds. Two to 3 minutes were required for eggs to settle 1 foot when the water was agitated. Application of these results to natural water indicates that more than 6 minutes would be required for eggs to reach bottom in still water 5 feet deep. It is quite probable that at times wave action and currents serve to distribute eggs widely before they eventually come to rest."

Also, Hunt (1953) relied on the adhesiveness of eggs when he collected them on glass plates submerged in water 3 ft deep.

Attachment structures consist of 3 basic types: polar caps, accessory attachment structures, and an external adhesive layer. Polar caps are attachment structures which are found at 1 or both poles or ends of many mayfly eggs. Most polar caps appear to be solid structures prior to their release into the water (Fig. 43, 52, 54). Upon entering the water the caps swell and expose the many threads with terminal knobs which function in attachment or anchorage of the egg (Fig. 41). In *Caenis* (Caenidae), *Ephoron* (Polymitarcidae), and the *interpunctatum* (Say) species-group of *Stenonema* (Heptageniidae), the cap is different. In *Caenis* the cap is composed of long, knob-terminated, spirally arranged threads which are coiled at the poles of the egg when the egg has not been in water. The cap may appear as a solid structure (Fig. 54, 56) or as a loose coil. When in water, the cap uncoils (Fig. 55) and the threads unwind or separate (Fig. 57), to serve as an attachment device.

The *interpunctatum* species-group in the genus *Stenonema* possesses caps that are merely very loose coils of thread encircling each pole of the egg (Fig. 16), and which uncoil upon contact with water.

The cap of *Ephoron* is unique in that it is a solid-structure type which is divided into a cluster of cylinderlike structures (Fig. 72–75). Each cylinder, according to Degrange (1960), is composed of many threads with terminal knobs. The effect of water is uncertain, but it probably causes the cap to swell and expand as in *Ephemerella* (Fig. 41).

The accessory attachment structures are situated on the lateral surfaces of the eggs. They may be in the form of suckerlike discs or plates (Fig. 24, 25, 45, 47), variously shaped adhesive projections (Fig. 30, 36), or coiled or uncoiled threads which frequently have terminal knobs (Fig. 1, 10, 39, 40). The coiled threads uncoil or spring out upon contact with water and become entangled with submerged objects or catch in small cracks or crevices. When coiled, the terminal knob frequently covers the coil, making it difficult to see, and chorionic sculpturing underneath the structure is usually much finer or absent.

Some eggs do not have polar caps or accessory attachment structures, attachment being accomplished by an adhesive layer which coats the egg and swells upon contact with water. Since this adhesive coating is often difficult to see, it is not always possible to determine its presence or absence. It is discussed herein only when noticeable, and one should not necessarily assume its absence if it is not discussed or if it cannot be found.

The micropylar device is the structure which allows the sperm to enter the egg. It is lateral in position, variable in number, and usually composed of 3 parts: the micropyle, the actual opening in the chorion which allows the sperm entrance; the sperm guide, an external depression in the chorion which usually lacks chorionic sculpturing, and which leads to and presumably aids in funneling sperm to the micropyle; and the micropylar canal, an internal tube leading from the micropyle into the egg (Fig. 4, 49, 53). One of the supplementary structures, the micropylar canal, has been noted in past literature (Korschelt 1884, Johannsen and Butt 1941). The sperm guide, the other supplementary structure, is apparently a term new to literature. Degrange (1956, 1960) used the term "micropyle" for the structure I refer to as the micropylar device.

In discussing the sperm guide and micropylar canal the terms "proximal" and "distal" are used, with the micropyle being the point of reference—thus distal to or proximal to the micropyle.

The presence of 2 or more micropylar devices is most common, and often it is difficult to count them exactly. Occasionally 2 micropylar devices will overlap, usually the micropyle of one being situated in the sperm guide of another. These are always atypical, and are not morphological features of any particular species or group of species.

The absence or modification of the sperm guide or micropylar canal results in 3 basic types of micropylar devices: a funnel-shaped sperm guide with micropylar canal short or lacking (Fig. 24, 27, 77, 79); an oval-shaped sperm guide with the micropylar canal situated to 1 side (Fig. 4, 49); and an elongate sperm guide, when present, followed by a more conspicuous micropylar canal (Fig. 15, 53, 71). In most cases the type of micropylar device remains constant within a family, and although useful for identification of eggs to family, it is seldom of value for generic and specific determinations.

In funnel-shaped micropylar devices (Fig. 24, 27, 77, 79) the micropyle is situated at the base and near the center of a funnel-shaped sperm guide. In the Leptophlebiidae, the micropyle is in a plane parallel to that of the chorion (Fig. 24, 27), and the presence or absence of the micropylar canal cannot be ascertained (Degrange (1960), has noted its presence by studying hatched eggs). In *Tortopus* (Polymitarcidae), however, the plane of the micropyle intersects that of the chorion, and here a short micropylar canal can be seen internal to the opening (Fig. 77, 79). These are the only groups known to have this type of micropylar device.

A more common micropylar device is that in which the micropyle is at 1 side of an oval-shaped sperm guide, and is followed by a micropylar canal of variable length (Fig. 4, 16, 49, 60). This micropylar device is found in the Ephemerellidae, Potamanthidae, Siphlonuridae, Tricorythidae, Baetidae (Degrange 1960), Oligoneuriidae (Degrange 1960), most Heptageniidae, and in *Ephoron* of the family Polymitarcidae. In *Ephoron virgo,* Degrange (1956, 1960) described a micropylar device consisting of a "half-skullcap" ("demi-calotte") followed by a canal, and established this as a separate type. In the 2 North American species of *Ephoron,* the micropylar device is different from *E. virgo.* The proximal portion of the micropylar canal is expanded, and it forms the "half-skullcap" (Fig. 75) described by Degrange. However, a typical oval sperm guide is also present, and

for this reason I include *Ephoron* with other groups having an oval sperm guide.

The third micropylar device, basically a conspicuous micropylar canal, is found in *Caenis*, Ephemeridae, and some *Stenonema*. The sperm guide may be present or absent. When present, it is either an elongate depression, usually free of chorionic sculpturing (Fig. 53, 62), or an elongate channel in the ridges of the reticulation (Fig. 71).

Dimensions (in microns) are given for most of the structures just described. When over 5μ, the dimensions are rounded off to the nearest whole number. However, when under 5μ, or over 5μ and with a narrow range, the measurements are expressed to the nearest $^1/_{10}\mu$.

Occasionally such inexact terms as "usually" are used in the keys or descriptions to note variations. However, the variation can be noted among the eggs from a single specimen, and by examining many of the eggs upon a slide, one can determine that condition which is most common.

Table 1 presents a summary of the morphological features found on the eggs discussed in this study. The taxa have not been arranged according to presently conceived phylogenetic relationships (Edmunds 1962), nor is the arrangement an attempt at a new concept of relationships. Rather it is arranged first by type of sperm guide, and second by type of accessory attachment structures. This is done so that one can more readily determine which features are common to which taxa.

SPECIES STUDIED

This study treats the following 60 species, which are distributed in 23 genera or subgenera and 10 families.

SIPHLONURIDAE
- *Siphlonurus alternatus* (Say)
- *S. mirus* Eaton

HEPTAGENIIDAE
- *Arthroplea bipunctata* McDunnough
- *Epeorus (Iron) suffusus* (McDunnough)
- *Heptagenia diabasia* Burks
- *H. hebe* McDunnough
- *H. juno* McDunnough
- *H. pulla* (Clemens)
- *Rhithrogena impersonata* (McDunnough)
- *R. sanguinea* Ide
- *Stenonema canadense* (Walker)
- *S. femoratum* (Say)
- *S. frontale* (Banks)
- *S. fuscum* (Clemens)
- *S. heterotarsale* McDunnough
- *S. lepton* Burks
- *S. minnetonka* Daggy
- *S. nepotellum* (McDunnough)
- *S. rubromaculatum* (Clemens)
- *S. tripunctatum* (Banks)
- *S. vicarium* (Walker)

AMETROPODIDAE
- *Siphloplecton basale* (Walker)

LEPTOPHLEBIIDAE
- *Habrophlebia vibrans* Needham ?
- *Habrophlebiodes americana* (Banks)
- *Leptophlebia* sp.
- *Paraleptophlebia adoptiva* (McDunnough)
- *P. debilis* (Walker)
- *P. mollis* (Eaton)
- *Thraulodes speciosus* Traver

EPHEMERELLIDAE
- *Ephemerella (Ephemerella) dorothea* Needham
- *E. (E.) excrucians* (Walsh)
- *E. (E.) invaria* (Walker)
- *E. (E.) subvaria* McDunnough
- *E. (Serratella) deficiens* Morgan
- *E. (Drunella) cornuta* Morgan
- *E. (D.) lata* Morgan
- *E. (D.) walkeri* Eaton
- *E. (Eurylophella) prudentalis* McDunnough
- *E. (E.) temporalis* McDunnough

TRICORYTHIDAE
- *Tricorythodes atratus* (McDunnough)
- *T. explicatus* (Eaton)
- *T. fallax* Traver
- *T. stygiatus* McDunnough

CAENIDAE
- *Caenis anceps* Traver
- *C. forcipata* McDunnough
- *C. jocosa* McDunnough
- *C. simulans* McDunnough

POTAMANTHIDAE
- *Potamanthus myops* (Walsh)
- *P. neglectus* Traver

EPHEMERIDAE
- *Ephemera guttulata* Pictet
- *E. simulans* Walker
- *E. varia* Eaton
- *Hexagenia limbata occulta* (Walker)
- *H. limbata venusta* Eaton
- *H. munda munda* Eaton
- *H. rigida* McDunnough

POLYMITARCIDAE
- *Ephoron album* (Say)
- *E. leukon* Williamson
- *Tortopus* sp. no. 1, Alabama
- *Tortopus* sp. no. 2, Texas

KEY TO FAMILIES

1. With 1 or more polar caps (Fig. 16, 43, 52, 54) 2
   Without polar caps (Fig. 9, 15, 37, 76) 8

2(1). With 2 or more polar caps (Fig. 16, 54, 59) ... 3
   With 1 polar cap (Fig. 43, 52, 56, 72) 5

3(2). Sperm guide oval (Fig. 16, 60) 4
   Sperm guide elongate or absent (Fig. 53, 56, 58) ..... most **Caenidae**

4(3). Each polar cap a loose coil of thread encircling the pole (may be more than 1 coil or cap per pole) (Fig. 16); accessory attachment structures, if present, coiled threads without terminal knobs ..... *Stenonema interpunctatum*-group, **Heptageniidae**
   Each polar cap appearing as a solid structure (Fig. 59); accessory attachment structures coiled threads with terminal knobs (Fig. 59, 60) ..... **Potamanthidae**

5(2). Chorion composed of many irregular, usually hexagonal, overlapping plates (Fig. 50–52); accessory attachment structures paired, uncoiled threads without terminal knobs ..... **Tricorythidae**
   Chorion not as above; if accessory attachment structures are threadlike, they occur singly, coiled, and with terminal knobs (Fig. 42, 44) 6

6(5). Sperm guide lacking (Fig. 56); chorionic sculpturing absent except under the cap ..... *Caenis anceps*, **Caenidae**
   Sperm guide oval (Fig. 43, 44, 73, 75); chorionic sculpturing present on entire egg, or if absent, cap as in Fig. 72–75 7

7(6). Preserved cap appearing as a single solid structure (Fig. 43); accessory attachment structures present, in the form of coiled threads with terminal knobs (Fig. 40, 42); chorion with small-mesh (3.1μ or less) reticulation of irregular polygons (Fig. 44); micropylar device situated in the middle half of the egg (Fig. 43) ..... most **Ephemerellidae**
   Polar cap appearing as a cluster of cylinders (Fig. 72–75); accessory attachment structures absent; chorion smooth or with a large-mesh reticulation (11–27μ) (Fig. 72); micropylar device located at the capped end of the egg (Fig. 72, 73, 75) ..... *Ephoron*, **Polymitarcidae**

8(1). With a large-mesh reticulation (greater than 10μ in length) (Fig. 17–20, 47, 67–71) 9
   With a small-mesh reticulation (less than 5μ long) (Fig. 31, 32, 63), or reticulation absent 11

9(8). Strands of reticulation are furrows, the mesh being a raised surface (Fig. 45, 46, 47); sperm guide oval (Fig. 47, 48, 49) ..... *Ephemerella (Eurylophella)*, **Ephemerellidae**

FAMILY	CHORION	ACCESSORY ATTACHMENT STRUCTURES	POLAR CAPS	SPERM GUIDE
LEPTOPHLEBIIDAE	Variable	Variable; Thraulodes only one with threads (& terminal knobs)	Absent	Funnel-shaped
POLYMITARCIDAE *Tortopus*	Punctate	Absent	Absent	Funnel-shaped
POLYMITARCIDAE *Ephoron*	Large-mesh reticulation or smooth	Absent	One	Oval-shaped
EPHEMERELLIDAE Sg. *Eurylophella* of *Ephemerella*	Large-mesh reticulation--furrows	Sucker-like plates?	Absent	Oval-shaped
EPHEMERELLIDAE Other Subgenera of *Ephemerella*	Small-mesh reticulation--ridges	Coiled threads with terminal knobs	One	Oval-shaped
POTAMANTHIDAE *Potamanthus*	Maculate	Coiled threads with terminal knobs	Two	Oval-shaped
TRICORYTHIDAE *Tricorythodes*	Overlapping plates	Paired threads without terminal knobs	One	Oval-shaped
SIPHLONURIDAE *Siphlonurus*	Maculate	Coiled threads without terminal knobs	Absent	Oval-shaped
AMETROPODIDAE *Siphloplecton*	Tuberculate	Coiled threads without terminal knobs	Absent	Micropylar Device unknown
HEPTAGENIIDAE *Arthroplea* *Epeorus* *Heptagenia* *Rhithrogena*	Variable	Variable	Absent	Oval-shaped
HEPTAGENIIDAE *Stenonema*, *interpunctatum* group	Sparsely tuberculate	Coiled threads without terminal knobs	Two-six	Oval-shaped
HEPTAGENIIDAE *Stenonema* except *interpunctatum* grp.	Sparsely tuberculate, tubercles often in a reticular arrangement	Absent	Absent	Elongate
EPHEMERIDAE *Ephemera*	Small-mesh reticulation or punctate	Absent	Absent	Elongate or absent
EPHEMERIDAE *Hexagenia*	Large-mesh reticulation	Absent	Absent	Elongate
CAENIDAE *C. anceps*	Smooth	Absent	One	Absent
CAENIDAE other species of *Caenis*	Variable	Absent	Two	Elongate or absent

Table 1.—A summary of the morphological features found on the eggs discussed in this study. The taxa have been arranged first by type of sperm guide, and second by type of accessory attachment structures.

Strands of reticulation are ridges (Fig. 67–71), or tubercles (Fig. 15, 17–20), the mesh being a depressed surface; sperm guide elongate (Fig. 15, 67, 71) 10

10(9). Strands of reticulation are ridges (Fig. 67–71); sperm guide an elongate channel in the ridges of the reticulation (Fig. 67–71) ..... *Hexagenia,* **Ephemeridae**

Strands of reticulation are tubercles (Fig. 15, 17–20); sperm guide elongate, but not in ridges of reticulation (Fig. 15, 17–20) ..... some *Stenonema,* **Heptageniidae**

11(10). Chorion densely tuberculate (Fig. 3); accessory attachment structures are coiled threads often in linear groupings surrounding 1 or both poles of the egg (Fig. 3) .. **Ametropodidae**

Chorion not tuberculate, or sparsely tuberculate (Fig. 7, 21); coiled threads, if present, never arranged in linear groupings as just described 12

12(11). Chorion completely covered with coiled, threadlike attachment structures (Fig. 1) ..... **Siphlonuridae**

Coiled threads never as dense as in Fig. 1 13

13(12). Sperm guide funnel-shaped (Fig. 23, 24, 27, 32, 77, 79) 14

Sperm guide oval (Fig. 4, 13), elongate (Fig. 21, 62, 66), or absent (Fig. 63) 15

14(13). Egg nearly circular, surrounded by an adhesive layer composed of many threads with terminal knobs (visible under 1250×) (Fig. 76, 80, 81); accessory attachment structures lacking; plane of micropyle at an angle to plane of chorion, thus the micropylar canal is apparent (Fig. 79) ... *Tortopus* **Polymitarcidae**

Egg ovoid, without an adhesive layer as just described; accessory attachment structures often present in various forms [coiled threads (Fig. 39), peglike structures (Fig. 30–36), suckerlike discs (Fig. 23–26)]; plane of micropyle parallel to that of the chorion, thus micropylar canal is absent or not apparent .. **Leptophlebiidae**

15(13). Sperm guide oval (Fig. 4, 5, 6, 8, 11, 13) ..... most **Heptageniidae**

Sperm guide elongate or absent (Fig. 21, 61–64, 66) 16

16(15). Chorion reticulate or punctate (Fig. 61–66) ... *Ephemera,* **Ephemeridae**

Chorion sparsely covered with small tubercles (Fig. 21) .... some *Stenonema,* **Heptageniidae**

SIPHLONURIDAE

Genus *Siphlonurus* Eaton

(Fig. 1, 2)

Form.—Ovoid, without polar caps.

Chorion.—(Fig. 2). Covered with many small dark round maculae, 2.3μ or less in diam.

Attachment Structures.—The entire surface of the egg is covered with groups of threads arranged in coils and lacking terminal knobs. Eggs of *S. mirus* Eaton laid in a 2-dr vial of water were held together and to the side of the vial by a thick gelatinous mass, visible to the naked eye. When this mass is magnified one can see a very dense network formed by an infinite number of small entwined threads. The female extruded the eggs continually until spent; the eggs did not exit as a single ball or mass, and therefore I am not certain that all the eggs would remain together when laid in a stream.

Degrange (1960), in discussing the attachment structures of *S. aestivalis* Eaton and *S. lacustris* Eaton, described a nipplelike structure covering each of the coils. When in water each nipple swells into a cluster of tenuous filaments making a projection on the surface of the rest of the adhesive layer. I could not find these structures on North American *Siphlonurus* eggs.

Micropylar Device.—Only one found, on an egg of *S. mirus,* and it agrees in form with those described by Degrange. Sperm guide oval, 18μ long by 15μ wide; micropylar canal 11.5μ long.

Although eggs of *S. alternatus, S. mirus, S. quebecensis* (Provancher), and *S. rapidus* McDunnough were available, only the first two cleared well enough for study. The diameter of the maculations is the only character that will separate the 2 species: 0.8μ or less in *S. alternatus,* 0.8–2.3μ in *S. mirus.*

HEPTAGENIIDAE

With the exception of the genus *Stenonema,* an oval-shaped sperm guide and lack of polar caps are the only characters typical of the family. Within *Stenonema,* the *interpunctatum*-group has an oval sperm guide and 2 polar caps; the other species-groups have an elongate sperm guide and no polar caps. The attachment structures vary from peglike in *Rhithrogena,* to coiled threads in *Heptagenia,* to an adhesive layer in most *Stenonema.* Two or more micropylar devices are present in all species studied.

KEY TO GENERA

1. Chorionic sculpturing and accessory attachment structures absent 2
   Chorionic sculpturing and or accessory attachment structures present (Fig. 4–21) 3
2. Sperm guide elongate or lacking (Fig. 22) ..... some ***Stenonema***
   Sperm guide oval ..... ***Epeorus***
3. Chorionic sculpturing a series of longitudinal ridges (Fig. 5) ..... ***Arthroplea***
   Chorionic sculpturing not as above 4
4. Chorionic sculpturing consists of peglike structures (Fig. 12, 13) ..... ***Rhithrogena***
   Chorionic sculpturing not as above 5
5. Sperm guide elongate (Fig. 15, 17–21), or absent .. some ***Stenonema***
   Sperm guide oval (Fig. 4, 6–9, 11, 16) 6
6. With 2–6 polar caps, each in the form of a loose coil of thread (Fig. 16) ..... some ***Stenonema***
   Polar caps lacking (Fig. 7, 9) ..... ***Heptagenia***

Arthroplea bipunctata McDunnough

(Fig. 5)

Form.—Oval, strongly tapered at each pole; without caps.

Chorion.—Sculpturing a series of longitudinal ridges, 2–4μ wide. The chorion must be much more fragile than that of other mayfly eggs, because several slides yielded no eggs without a cracked or broken chorion.

Attachment Structures.—Since no accessory attachment structures were found, attachment must occur by means of an adhesive layer (although this was not observed).

Micropylar Device.—Sperm guide oval, 9.5–11.5μ long by 5.5–7.5μ wide; micropylar canal 7.5–9.5μ long. Although averaging 5, as many as 10 devices have

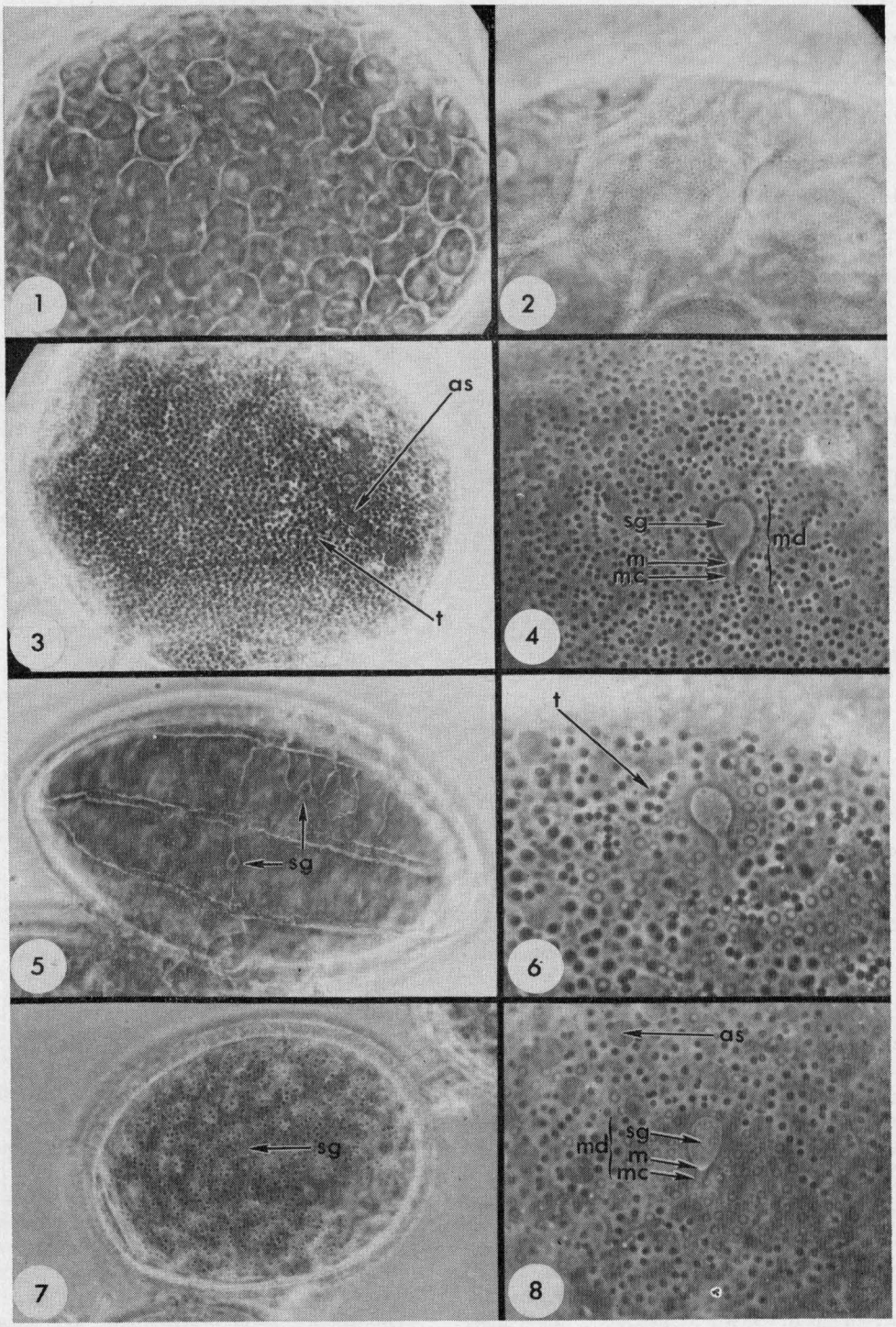

FIG. 1, 2.—*Siphlonurus alternatus.* 1, egg, covered with coiled threadlike attachment structures (300×). 2, chorionic maculations (938×). FIG. 3.—*Siphloplecton basale,* egg (300×). FIG. 4.—*Heptagenia diabasia,* micropylar device (750×). FIG. 5.—*Arthroplea bipunctata,* egg (300×). FIG. 6.—*H. hebe,* micropylar device (938×). FIG. 7, 8.—*H. juno.* 7, egg (300×). 8, micropylar device (750×) .

been found scattered throughout the midregion of the egg.

Epeorus (Iron) suffusus McDunnough

Form.—Ovoid, without polar caps.

Chorion.—Smooth, with no sculpturing.

Attachment Structures.—None found.

Micropylar Device.—Sperm guide oval, 11–16μ long by 8–11μ wide; micropylar canal 7–13μ long.

Degrange (1960) studied *E. assimilis* Eaton and *E. alpicola* Eaton and likewise found a smooth chorion and a lack of attachment structures.

Genus *Heptagenia* Walsh

(Fig. 4, 6–11)

The eggs of *H. hebe, H. rusticalis* McDunnough, *H. lucidipennis* (Clemens), *H. aphrodite* McDunnough, *H. maculipennis* Walsh, *H. elegantula* (Eaton), *H. marginalis* (Banks), *H. pulla,* and *H. flavescens* (Walsh) were studied by Smith (1935). The eggs of *H. coerulans* (Rostock), *H. lateralis* (Curtis), and *H. sulphurea* (Müller) were studied by Degrange (1960).

All known *Heptagenia* eggs are ovoid and lack polar caps. The chorion is covered with many unevenly scattered tubercles (Fig. 6) which vary in diameter. On the *Heptagenia* eggs of this study, there are areas in which the tubercles have been replaced by ringlike markings (Fig. 6, 8), and the size and abundance of these areas vary among the species. Obscure maculations form a background to the obvious pattern presented by the tubercles and ringlike markings. *Heptagenia* eggs characteristically have attachment structures in the form of threads (Fig. 9, 10) (0.5μ in diam except in *H. pulla*) which are often so tightly coiled that they appear as large maculations (Fig. 8). Palmen (1884), Smith (1935), and Degrange (1960) correctly reported terminal knobs for these threads. The threads are usually concentrated at 1 or both poles, but may be found also on the lateral surfaces of the egg.

KEY TO SPECIES

1. Tubercles usually less than 1μ in diam (Fig. 9–11); attachment threads mostly restricted to the poles of the egg (Fig. 9, 10) ..... ***pulla***
   Tubercles greater than 1μ in diam (Fig. 4, 6–8); attachment structures not restricted to the poles of the egg (Fig. 7, 8) 2
2. Ringlike markings not abundant, occurring singly or in small groups of 2–6 (Fig. 4) ..... ***diabasia***
   Ringlike markings abundant, concentrated into large groups and frequently covering up to ⅓ or more of a given surface (Fig. 6–8) ..... ***hebe*** and ***juno***

Heptagenia diabasia Burks

(Fig. 4)

Chorion.—Tubercles 1.2–1.5μ in diam; ringlike markings not abundant, usually isolated or in groups of about 2–6.

Attachment Structures.—Coiled threads concentrated at the poles, but also occurring in the midregion of the egg.

Micropylar Device.—Sperm guide oval, with a rim 1.2–1.5μ wide. Inside dimensions of sperm guide are 11–15μ long by 7–10μ wide; micropylar canal 6–14μ long.

Heptagenia hebe McDunnough and *Heptagenia juno* McDunnough

(Fig. 6–8)

Chorion.—Tubercles 1.2–2.3μ in diam; ringlike markings abundant, covering as much as ½ of a given surface, concentrated in large groups or occurring singly.

Attachment Structures.—Coiled threads scattered about the surface of the egg, not restricted to poles.

Micropylar Device.—Sperm guide oval, 8.5–12μ long by 6–8.5μ wide; micropylar canal 8–17μ long.

Heptagenia pulla (Clemens)

(Fig. 9–11)

Chorion.—Tubercles usually less than 1μ in diam. Ringlike markings much less abundant than in other species, but may occur in large concentrations.

Attachment Structures.—Coiled threads mostly restricted to the poles, very few occurring in the midregion; threads much thicker (1.5μ) than those on other species (0.5μ).

Micropylar Device.—Sperm guide oval, 12–21μ long by 10–16μ wide; micropylar canal present but rarely distinguishable, 9μ long.

Genus *Rhithrogena* Eaton

(Fig. 12, 13)

Form.—Ovoid, without polar caps.

Chorion and Attachment Structures.—The chorion is covered with short peglike structures (3.5–5μ long) which undoubtedly serve for attachment as do those of some Leptophlebiidae.

Micropylar Device.—Sperm guide oval, 11–17μ long by 8–10μ wide; micropylar canal 11–17μ long. The sperm guide possesses a thick rim, and the measurements given are inside dimensions.

Characters could not be found to separate the eggs of *R. impersonata* and *R. sanguinea.*

Genus *Stenonema* Traver

(Fig. 14–22)

Smith (1935) and Spieth (1947) correctly noted that there are 2 types of eggs in the genus, that of the *interpunctatum*-group (species-groups as set up by Burks 1953) with a coiled thread at each pole, and that of the other species-groups lacking threads and possessing a gelatinous coat that swells when the egg is deposited in water.

With the exception of the *interpunctatum*-group, the eggs of *Stenonema* can be readily recognized by the type of micropylar device. The sperm guide (usually absent in *S. vicarium*) is an elongate depression in which the sculpturing persists (Fig. 20), and which often possesses a proximal "hood" (Fig. 15, 17). I need to study eggs in water, but I think this hood is formed by the adhesive layer—thus the distal portion of the sperm guide is without an ad-

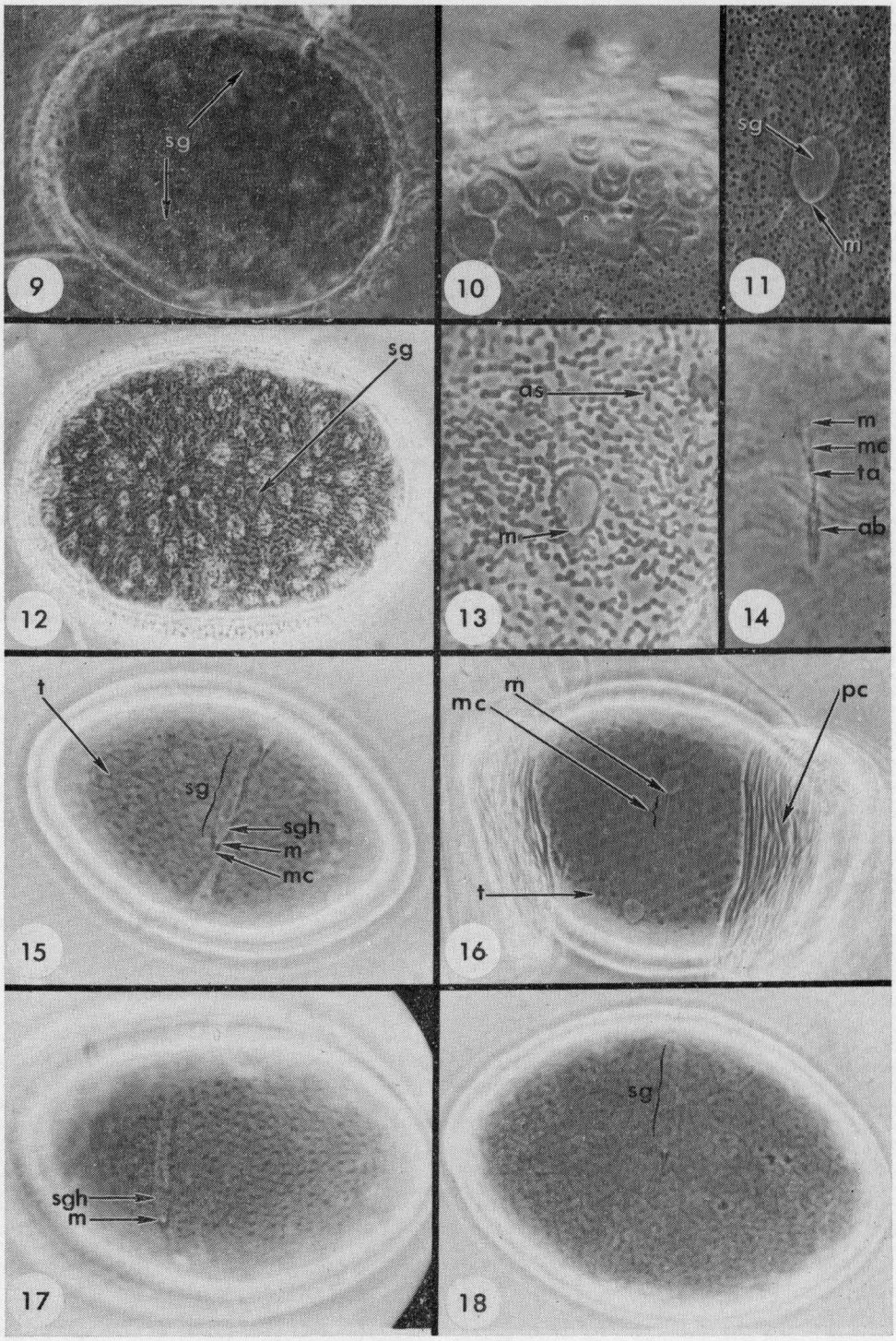

FIG. 9–11.—*Heptagenia pulla.* 9, egg (300×). 10, coiled attachment threads at pole (750×). 11, micropylar device (750×). FIG. 12, 13.—*Rhithrogena impersonata.* 12, egg (300×). 13, micropylar device (750×). FIG. 14.—*Stenonema rubromaculatum,* micropylar canal (750×). FIG. 15.—*S. nepotellum,* egg (300×). FIG. 16.—*S. canadense,* egg (300×). FIG. 17.—*S. lepton,* egg (375×). FIG. 18.—*S. rubromaculatum,* egg (300×).

hesive layer covering it. The distal end of the sperm guide fades and is often obscure; therefore it is frequently difficult to measure its length accurately. The micropylar canal tapers distally, and it frequently has a terminal appendage (Fig. 14) which may have an apical "brush." I am unable to make any decisions concerning the function and nature of this appendage and have not included it in length measurements of the micropylar canal.

The chorion of the *tripunctatum, pulchellum,* (Walsh), and *terminatum* (Walsh) species-groups is sparsely covered with short, irregularly shaped tubercles, many of which are often arranged in a reticular pattern of large, irregular-polygonal mesh. The chorion of the *vicarium*-group is smooth. The only attachment structure is an adhesive layer which presents a striated appearance in preserved material.

The eggs of the *interpunctatum*-group possess 2–6 polar caps, each formed by a single thread coiled about the pole (Fig. 16). The micropylar device, with an oval sperm guide, is typical of the family. The chorion is sparsely covered with tubercles which are not as irregular in shape as those of the other species-groups.

Because *Stenonema* is a large genus, and adults of its species often vary considerably in their own external morphology, the keys and descriptions for the species are given with some reservation. Enough material of species with a wide distribution was not available, and therefore the reliability of the keys and descriptions is not known. Although these must serve at best as a foundation for future studies of the genus, I am quite sure that characters used to distinguish the genus from other genera in the family are reliable.

KEY TO SPECIES

1. With 2–6 polar caps (Fig. 16) ..... ***canadense***
   Without polar caps 2
2. Chorion smooth, without sculpturing (Fig. 22) 3
   Chorionic sculpturing in the form of short tubercles, often with a reticular pattern of arrangement (Fig. 15, 17–21) 4
3. Sperm guide usually lacking; micropylar canal 8–15μ long; egg nearly circular in form ..... ***vicarium***
   Sperm guide present, elongate (Fig. 22); micropylar canal 13–18μ long; egg ovoid in form ..... ***fuscum***
4. Tubercles not in a reticular pattern (Fig. 21) ..... ***femoratum***
   Tubercles arranged in a reticular pattern (Fig. 15, 17–20) 5
5. Micropylar canal usually 12–14μ long 6
   Micropylar canal usually 5–12μ long 7
6. Sperm guide with basal hood (Fig. 15) ... ***nepotellum***
   Sperm guide without basal hood (Fig. 19, 20) ..... ***tripunctatum***
7. Micropylar canal 10–12μ long; sperm guide with basal hood 7–23μ long (Fig. 17) ..... ***lepton***
   Micropylar canal 5–9μ long; sperm guide with short basal hood (3–6μ long) or hood absent (Fig. 18) ..... ***rubromaculatum***

CANADENSE-Group:

Stenonema canadense (Walker)

(Fig. 16)

Form.—Ovoid, with 2–6 polar caps.

Chorion.—Sparsely covered with short tubercles ranging from 1–4μ in diam.

Attachment Structures.—Each of the polar caps (Fig. 16, with 2 caps) is formed by a single thread coiled about the pole, which, according to Smith (1935), can be outstretched to a length of 2 in. or more. Smith noted that the thread is attached at a small protuberance on the chorion. Smith noted also the presence of smaller coils of thread which are usually situated near the margins of the caps.

A specimen from Maine, tentatively determined as *S. canadense,* yielded eggs with 2 and occasionally 3 coils of threads arranged on one or both poles.

Micropylar Device.—Sperm guide oval, 13–17μ long by 11–13μ wide; micropylar canal 17–25μ long.

Eggs of *S. frontale, S. heterotarsale,* and *S. minnetonka* did not differ from *S. canadense* in details of the cap (1/pole) and micropylar device; the chorion could not be satisfactorily observed.

PULCHELLUM-Group:

Stenonema nepotellum (McDunnough)

(Fig. 15)

Form.—Ovoid, tapered toward the poles; without polar caps.

Chorion.—Tubercles arranged in a reticular pattern of large irregular-polygonal mesh (19–27μ long).

Micropylar Device.—Sperm guide elongate (42–61μ long), tapering distally, and with a proximal hood 12–20μ long; micropylar canal 12–14μ long.

Stenonema rubromaculatum (Clemens)

(Fig. 14, 18)

Like *S. nepotellum* except the sperm guide does not taper distally, the proximal hood is short (3–6μ long) or lacking, and the micropylar canal is 5–9μ long.

TERMINATUM-Group:

Stenonema lepton Burks

(Fig. 17)

Form.—Ovoid, tapered toward poles; without polar caps.

Chorion.—Tubercles arranged in a reticular pattern of large irregular-polygonal mesh (23–31μ long).

Micropylar Device.—Sperm guide elongate (31–54μ long), not tapering distally, and with a proximal hood (7–23μ long); micropylar canal 10–12μ long.

TRIPUNCTATUM-Group:

Stenonema femoratum (Say)

(Fig. 21)

Form.—Ovoid, not tapered at poles; without polar caps.

Chorion.—Tubercles randomly scattered, having no particular pattern of arrangement.

Micropylar Device.—Sperm guide elongate (35–54μ long), tapering distally, and without a proximal hood; micropylar canal 10–11μ long.

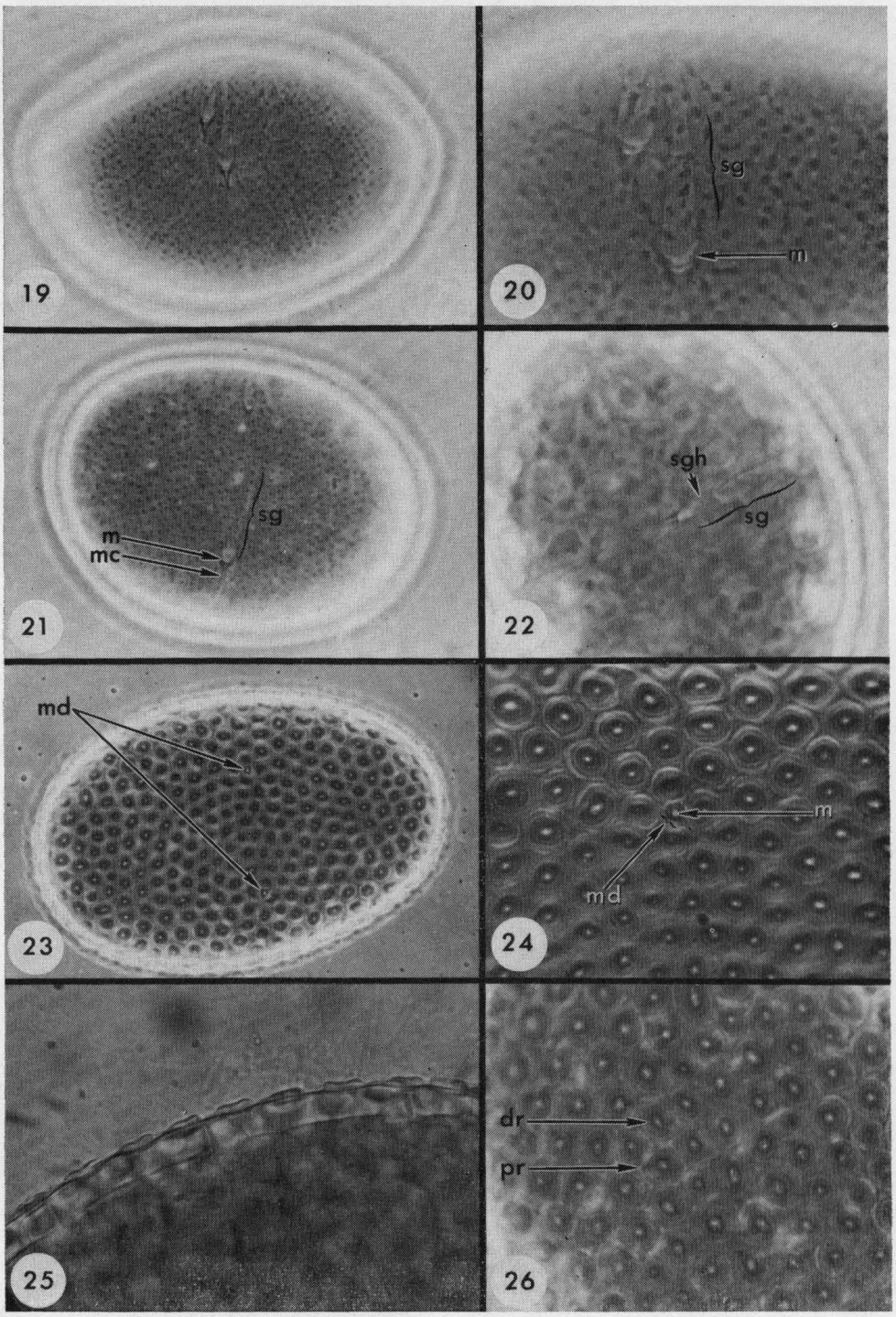

FIG. 19, 20.—*Stenonema tripunctatum.* 19, egg (300×). 20, micropylar device (750×). FIG. 21.—*S. femoratum,* egg (300×). FIG. 22.—*S. fuscum,* micropylar device (375×). FIG. 23, 24.—*Habrophlebiodes americana.* 23, egg (300×). 24, microplyar device (750×). FIG. 25, 26.—*H. americana.* 25, tangential view showing sucker-like discs in relief (750×). 26, Surface view showing pseudoreticulation (750×).

Stenonema tripunctatum (Banks)

(Fig. 19, 20)

Form.—Ovoid, slightly tapered toward poles; without polar caps.

Chorion.—Tubercles arranged in a reticular pattern of large irregular-polygonal mesh (17–23μ long).

Micropylar Device.—Sperm guide elongate (38–54μ long), tapering distally, and without a proximal hood; micropylar canal 12–14μ long.

VICARIUM-Group:

Stenonema fuscum (Clemens)

(Fig. 22)

Form.—Ovoid, without polar caps.

Chorion.—Smooth, sculpturing absent.

Micropylar Device.—Sperm guide elongate (50–62μ long), not tapering distally, and with a basal hood (5–17μ long); micropylar canal 13–18μ long.

Stenonema vicarium (Walker)

Like *S. fuscum* except nearly circular in form, sperm guide usually lacking, and micropylar canal 8–15μ long.

AMETROPODIDAE

Siphloplecton basale (Walker)

(Fig. 3)

Form.—Distorted, without polar caps. The only material available was collected in 1950, and preserved in 85% ETOH. I could not determine if the distortion of these eggs is natural or caused by preservation. Smith (1935) indicates that the eggs of *S. basale* (Walker), *S. signatum* (Traver), and *S. speciosum* Traver are ovoid.

Chorion.—Tuberculate; tubercles 2μ or less in height, 2–3.5μ wide.

Attachment Structures.—Coiled threads, without terminal knobs, occurring singly or in linear groupings which often encircle 1 or both poles of the egg. When single, the diameter of the coil is approximately one-half that of the coils occurring in linear groupings.

Micropylar Device.—Unknown.

LEPTOPHLEBIIDAE

There is such a wide diversity of chorionic sculpturing and attachment structures within this family that it is impossible to use these features for recognition of the family. However, the type of micropylar device, the lack of polar caps, and the ovoid form (except the nearly rectangular eggs of *Thraulodes speciosus*) are constant features characteristic of the family.

There are 2 or 3 micropylar devices present, and these are situated about the equatorial region of the egg. The micropyle is situated at the base and near center of a funnel-shaped sperm guide; the micropylar canal is apparently lacking. Measurements have been given for the diameter of the top rim of the funnel (which is at the surface of the egg) and for the diameter of the micropyle.

KEY TO GENERA AND SPECIES

1. Surface of egg evenly covered with coiled threadlike attachment structures (Fig. 39) ..... ***Thraulodes speciosus***
   Egg without threadlike attachment structures arranged like those in Fig. 39 2
2. Chorionic sculpturing a series of longitudinal ridges or bands (Fig. 27–29) .... ***Habrophlebia vibrans*** ?
   Chorionic sculpturing never in the form of longitudinal ridges, but may be raised suckerlike discs, tubercles, peglike projections or a reticulation (Fig. 23–26, 32–38) 3
3. Chorionic sculpturing in the form of tubercles or raised suckerlike discs (Fig. 23–26, 37, 38) 5
   Chorionic sculpturing reticulate or peglike, or both (Fig. 30–36) 4
4. Chorionic sculpturing a small-mesh reticulation (Fig. 31, 32); attachment structures are stout (3.5–5.5μ wide) peglike translucent projections which are frequently clumped in groups of 2–6 or more, and which do not "mushroom" when in water (Fig. 30, 32) ..... ***Leptophlebia*** sp.
   Chorionic reticulation absent; attachment structures are slender (1.1–1.5μ wide) peglike projections which are evenly scattered about the surface of the egg, and which develop a mushroom shape when in water (and occasionally, to some extent in alcohol) (Fig. 33–36) ..... ***Paraleptophlebia adoptiva*** and ***P. mollis***
5. Raised surfaces are suckerlike discs averaging 5.4–6.9μ in diam (Fig. 23–26) ..... ***Habrophlebiodes americana***
   Raised surfaces are tubercles only, not suckerlike discs, averaging 2.3–3.8μ in diam (Fig. 37, 38) ..... ***Paraleptophlebia debilis***

Habrophlebia vibrans Needham ?

(Fig. 27–29)

Chorion.—Chorionic sculpturing a series of wide (11.5–13.5μ), elevated, longitudinal bands which are occasionally branched, and are separated by a space of 7–10μ. On the lateral margins of the bands many small fingerlike projections occur (0.7–3.1μ long), the purpose of which is unknown. With the use of a Carl Zeiss Photomicroscope equipped with the Nomarski interference-contrast attachment (shows relief), it was determined that the longitudinal bands consist of 3 ridges, 1 median and 2 lateral (Fig. 27, 28).

Attachment Structures.—Degrange described attachment structures as being refractive granular masses (20–28μ in diam) situated in the middle and posterior regions of the egg. No such structures could be found in the available material. The longitudinal ridges, as well as their lateral projections, most likely have something to do with attachment—no other structures could be found, and fresh material was unavailable.

Micropylar Device.—Sperm guide funnel shaped, rim 8–13μ in diam; micropyle 1.5–2μ in diam (Fig. 27, 29).

The determination of this species is questionable, since it is based upon a single female collected in New York State.

Habrophlebiodes americana (Banks)

(Fig. 23–26)

Chorion.—Reticulation absent. However, there is

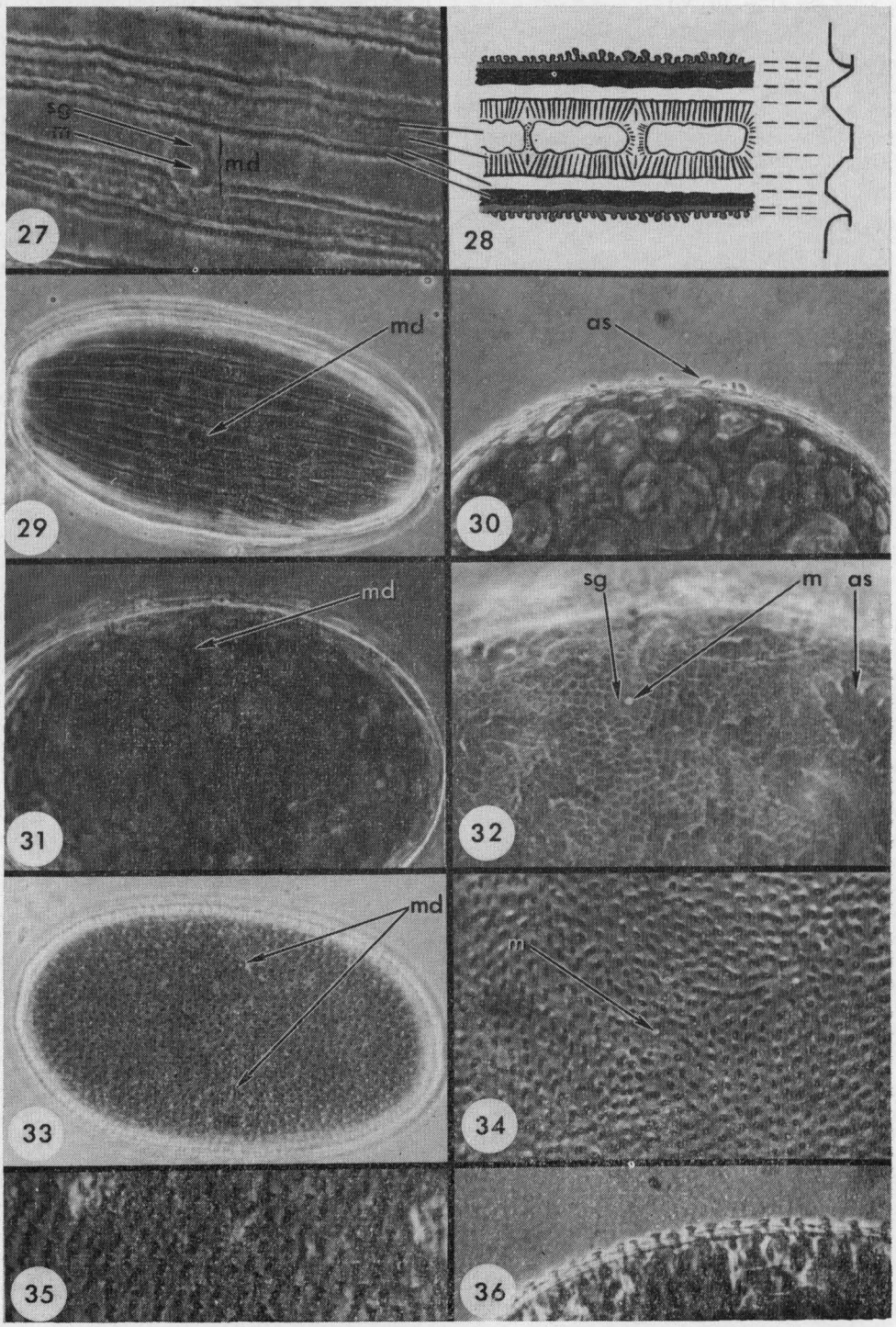

FIG. 27–29.—*Habrophlebia vibrans* ?. 27, micropylar device (750×). 28, diagrammatic view and projected cross-section of chorionic ridges. 29, egg (300×). FIG. 30–32.—*Leptophlebia* sp. 30, tangential view showing peglike attachment structures in relief (300×). 31, egg (300×). 32, micropylar device (750×). FIG. 33.—*Paraleptophlebia adoptiva*, egg (300×). FIG. 34–36.—*P. mollis*. 34, micropylar device (750×). 35, peglike attachment structures. Eggs laid in water, slide-mounted 5 min later (750×). 36, same as Fig. 35, tangential view (750×).

an apparent reticulation which is not readily discernible, and which should not be confused with a true reticulation. This pseudoreticulation is composed of 6-sided mesh (occasionally 5- or 7-sided) including a distinct light spot at the joints of the strands (Fig. 26). The spots are 0.8–1.2μ in diam, whereas the strands are mere lines the width being immeasurable even under oil immersion (1250×). It appears that this pseudoreticulation is formed by the close fitting nature of the circular attachment structures to be described.

Attachment Structures.—Suckerlike plates which are usually circular in form, but often vary from an irregular circle to nearly a rectangle. The outside dimensions of the raised portion of the plates (Fig. 25) range from 4.6 to 9.2μ, the average being between 5.4μ and 6.9μ. The width (thickness) and height of the rim of the suckerlike plates both range between 1.5–2.3μ.

Nothing is known about the adhesive nature of these eggs, but it is suspected that these plates act as suckers, aided by an adhesive substance coating the egg.

Micropylar Device.—Sperm guide funnel shaped, inserted among the closely spaced plates. Although the micropyle is nearly a perfect circle (1.5–2.3μ in diam), the rim of the sperm guide is a very irregularly shaped polygon (3.8–6.2μ long), (Fig. 23, 24).

Leptophlebia sp.

(Fig. 30–32)

Chorion.—The chorion bears a small-mesh (3.8μ or less long), irregular polygonal reticulation formed by ridges 0.5–1.5μ thick (Fig. 32). Morgan (1913) described in *L. cupida* (Say) the presence of irregularly scattered pits and bosses, but did not describe the actual reticular pattern.

Attachment Structures.—Both Morgan (1913) and Smith (1935, *L. austrina* (Traver), *L. cupida* (Say), *L. grandis* (Traver), and *L. nebulosa* (Walker)) noted the presence of stout peglike projections, Smith correctly noted that they are translucent. They occur singly or in groups of 2–6 or more, are 5.5–10μ long by 3.5–5.5μ wide, and are found scattered over the entire surface (Fig. 30, 32). Smith remarks that "in water these projections stand out at right angles to the surface of the egg and adhere even to glass."

Micropylar Device.—Sperm guide funnel shaped, rim 5.8μ in diam; micropyle ovoid, 1.5–2.7μ long (Fig. 31, 32).

The egg of *L. marginata* (L.), described and figured by Degrange (1960), is very similar to the one just described, except the peglike projections are not grouped. Smith (1935) described *L. johnsoni* McDunnough as being unlike the other 4 *Leptophlebia* studied by him, its egg having "a reticular pattern of sinuous ridges, and translucent projections stand up like fence posts wherever these ridges branch."

Genus ***Paraleptophlebia*** Lestage

(Fig. 33–38)

Smith (1935) stated that *P. adoptiva* (McDunnough), *P. debilis* (Walker), *P. moerens* (McDunnough), *P. mollis* (Eaton) and *P. memorialis* (Eaton) (as *P. pallipes* (Hagen)) "all have ellipsoid eggs, 0.18–0.20 mm by 0.10 mm. In preserved material the chorion is thickly covered with many small bosses and by focusing carefully, a few small finger-like projections may be seen." His techniques apparently did not allow him to observe that his "bosses" were actually end views of the projections. He believed that these bosses must spring out when in water to form the narrow projections (cilia) described by Morgan (1913). I studied 3 of the species he did, and 2 (*P. adoptiva* and *P. mollis*) possess peglike (fingerlike) projections, the third (*P. debilis*) possesses small tubercles (bosses). Both Morgan (1913, *Leptophlebia* sp.?) and Degrange (1960, *P. submarginata* (Stephens)) record similar projections. The micropyles are all typical of the family, and no generic characters could be found to separate *Paraleptophlebia* from the other genera of Leptophlebiidae.

Paraleptophlebia adoptiva (McDunnough) and ***P. mollis*** (Eaton)

(Fig. 33–36)

Chorion and Attachment Structures.—The entire surface of the egg is covered with short peglike projections (Fig. 33, 34), doubtlessly adhesive in nature. When eggs are laid in water, the ends of these projections swell, and the projections become "mushroom"-shaped (Fig. 35, 36) thus forming a greater surface area for adhesion. The projections are 3.1–3.8μ long (including the cap when formed) by 1.1–1.5μ wide (not the cap). The cap itself is up to 3.8μ wide. It may be possible to obtain larger measurements for the projections if the eggs are allowed to remain in water for more than 5 min.

Micropylar Device.—Sperm guide funnel shaped, rim 5.8μ in diam; micropyle 1.9–3.1μ in diam (Fig. 33, 34).

Paraleptophlebia debilis (Walker)

(Fig. 37, 38)

Chorion.—Covered with many small circular tubercles 2.3–3.8μ in diameter. Much smaller tubercles, 1.5μ or less in diam, occur intermittently among the larger ones. Relatively wide striations weave among the tubercles.

Attachment Structures.—None, unless the tubercles on the chorion act as adhesive devices.

Micropylar Device.—Sperm guide funnel shaped, rim 5.4–6.9μ in diam; micropyle 1.5μ in diam (Fig. 37, 38).

Thraulodes speciosus Traver

(Fig. 39)

Form.—Nearly rectangular.

Chorion.—Covered with irregular circular maculations 0.8–3.1μ in diam.

Attachment Structures. — Threadlike attachment

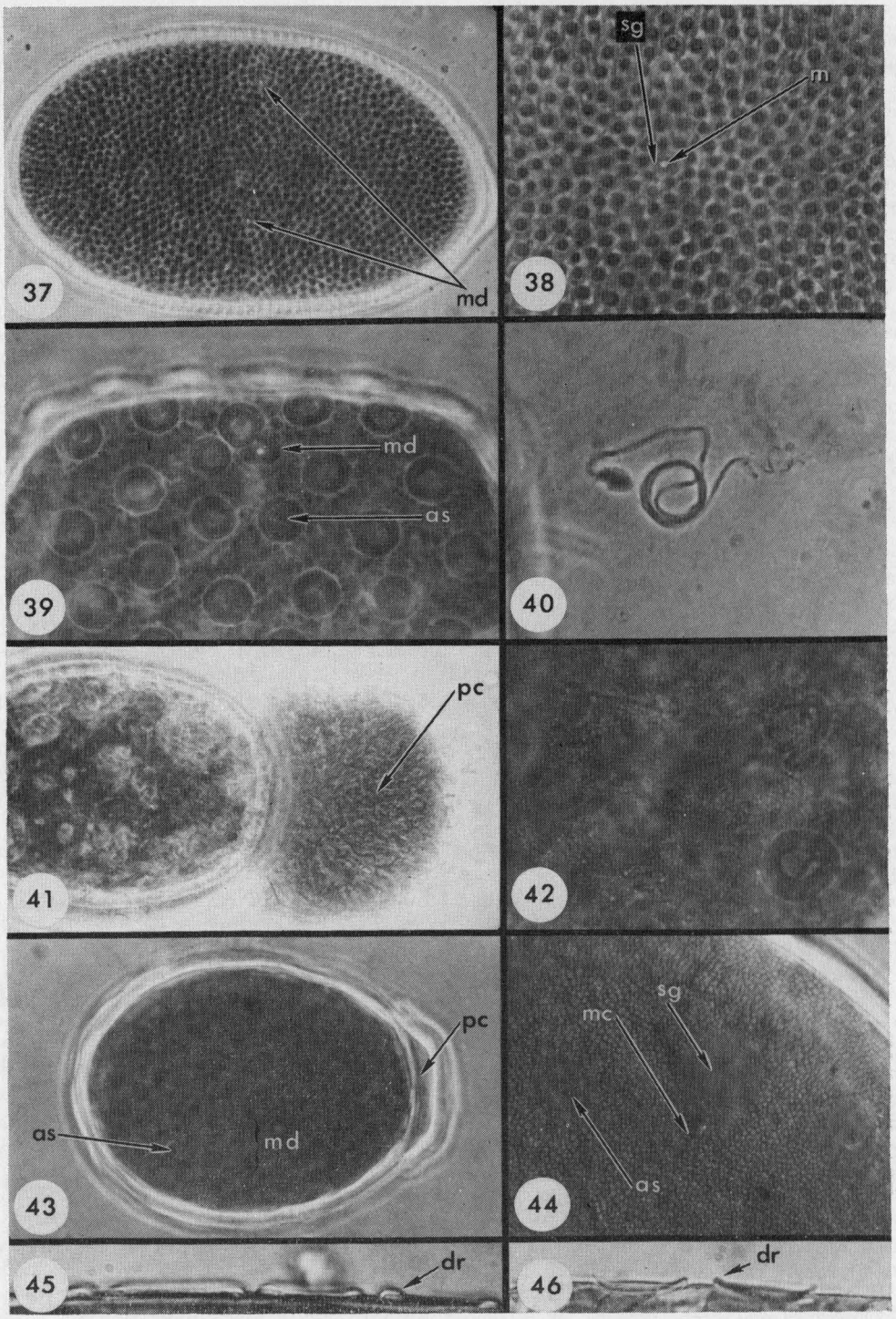

FIG. 37, 38.—*Paraleptophlebia debilis.* 37, egg (300×). 38, micropylar device (750×). FIG. 39.—*Thraulodes speciosus,* egg (750×). FIG. 40.—*Ephemerella* (*Serratella*) *deficiens,* coiled threadlike attachment structure showing terminal knob; removed from egg (750×). FIG. 41.—*E.* (*Ephemerella*) *invaria*?, expanded polar cap. Eggs laid in water, removed to 70% ETOH 12 hr later (300×). FIG. 42.—*E.* (*S.*) *deficiens,* chorion and attachment structures (750×). FIG. 43, 44.—*E.* (*Drunella*) *cornuta.* 43, egg (300×). 44, micropylar device (750×). FIG. 45, 46.—*E.* (*Eurylophella*) *prudentalis.* 45, tangential view showing suckerlike plates. Eggs laid in water, removed to 70% ETOH 12 hr later (938×). 46, same view as Fig. 45, eggs from preserved specimen (750×).

structures, covering a circular area 8.5–10.7μ in diam when coiled, are evenly distributed over the chorion. No uncoiled threads could be found. However, it appears that they are terminated by very small knobs. An adhesive layer is also apparent. Traver and Edmunds (1967) discussed the eggs of 7 species of *Thraulodes,* and it appears that the presence of many coiled threads distributed about the chorion is a feature which will distinguish *Thraulodes* eggs from all other known Leptophlebiidae eggs.

Micropylar Device.—Typical of the family, except the micropyle (1.5μ in diam) sits at the bottom of a funnel-shaped sperm guide, which is much deeper than in other leptophlebiids. Only 1/egg, the micropylar device is most commonly found very close to one of the coiled threads.

EPHEMERELLIDAE

Genus *Ephemerella* Walsh

A single polar cap, coiled threads with terminal knobs, ovoid form, and an ovoid sperm guide will serve to distinguish the Ephemerellidae (except *Ephemerella (Ephemerella) maculata* Traver (described by Smith 1935) and the subgenus *Eurylophella*) from other North American families of Ephemeroptera. Smith (1935) studied 25 species, representing all of the North American subgenera. He indicated that only *E. maculata* and the subgenus *Eurylophella* are atypical, having a nearly rectangular form and lacking the coiled threads and polar cap typical of the rest of the family. However, *Eurylophella* does have a micropylar device typical of the family; that of *E. maculata* is unknown. The eggs studied by Degrange (1956) are also typical of the family.

The eggs of the subgenera of *Ephemerella* other than *Eurylophella* all possess 1 polar cap (Fig. 43), which swells and separates when in water, revealing a thick mass of short threads with terminal knobs (Fig. 41). The accessory attachment structures are coiled threads, each with a terminal knob; the knob is a fibrillous disc with the thread attached at the center (Fig. 40).

The micropylar devices of all subgenera consist of an oval sperm guide, a micropyle, and an elongate micropylar canal; and they vary considerably in their dimensions. In all cases there is more than 1 micropylar device present, and these are usually situated in the middle half of the egg.

KEY TO SUBGENERA

1. Polar cap and knob-terminated coiled threads present (Fig. 40–44) 2
   Polar cap and knob-terminated coiled threads absent Fig. 47) ..... ***Eurylophella***
2. Oval areas, in which the reticulation is finer or absent, usually numbering 6 or less on a given surface, and providing the attachment point for the coiled threads (Fig. 44) ..... ***Drunella*** and ***Ephemerella***
   Oval areas usually numbering 45 or more; coiled threads not as frequent as, and not always attached in, the oval areas (Fig. 42) . . ***E. (Serratella) deficiens***

Subgenera *Ephemerella* Walsh and *Drunella* Needham

Four species of *Ephemerella (dorothea, excrucians, invaria,* and *subvaria)* and 3 species of *Drunella (cornuta, lata,* and *walkeri)* were studied and found indistinguishable even at the subgeneric level. One species of the subgenus *Serratella (deficiens)* was found to be separable from the 7 species just mentioned of *Ephemerella* and *Drunella.* Smith (1935) likewise found eggs of most species of Ephemerellidae to be inseparable.

Ephemerella (Drunella) cornuta Morgan

(Fig. 43, 44)

The egg of this species is typical of those of the 7 species of the subgenera *Ephemerella* and *Drunella* studied, and will suffice as a description for both subgenera.

Form.—Ovoid, with 1 polar cap.

Chorion.—Finely reticulated with an irregular polygonal mesh measuring up to 3.1μ long. Oval areas with reticulation much finer or absent, scattered about on the chorion; usually numbering less than 6, and never more than 12, on a given surface.

Attachment Structures.—Two types: a single polar cap; and several coiled threads with terminal knobs, each thread being attached in 1 of the oval areas just described. (Fig. 43 and 44, and similar to Fig. 40.)

Micropylar Device.—Sperm guide oval, 20–22μ long by 17–18μ wide; micropylar canal 3–5μ long (Fig. 44).

Ephemerella (Serratella) deficiens Morgan

(Fig. 40, 42)

Form.—Ovoid, with a single polar cap.

Chorion.—Finely reticulated with an irregular polygonal mesh measuring up to 3.1μ in length. Scattered about on the surface are many oval areas completely void of the reticulation. There are 45 or more of these areas on a given surface, and this feature will distinguish *E. deficiens* from the species of the subgenera *Ephemerella* and *Drunella* mentioned earlier. The boundaries of these areas are difficult to distinguish, but the diameters range between 8–19μ (Fig. 42).

Attachment Structures.—Two types: a single polar cap; and several coiled threads with terminal knobs, the threads not as frequent as, and not always attached in, the oval areas in the chorion (Fig. 40, 42).

Micropylar Device.—Sperm guide oval, 19μ long, 11.5μ wide; micropylar canal 6.2–7.7μ long.

Subgenus *Eurylophella* Tiensuu

(Fig. 45–49)

The lack of polar caps and coiled threads, the rectangular form and presence of a large-mesh reticulation formed by furrows, serve to separate eggs of the subgenus *Eurylophella* from all other known eggs of the Ephemerellidae. The chorion of *Eurylophella* eggs is covered with irregularly shaped polygonal plates with raised edges (Fig. 45, 46, 47) and length

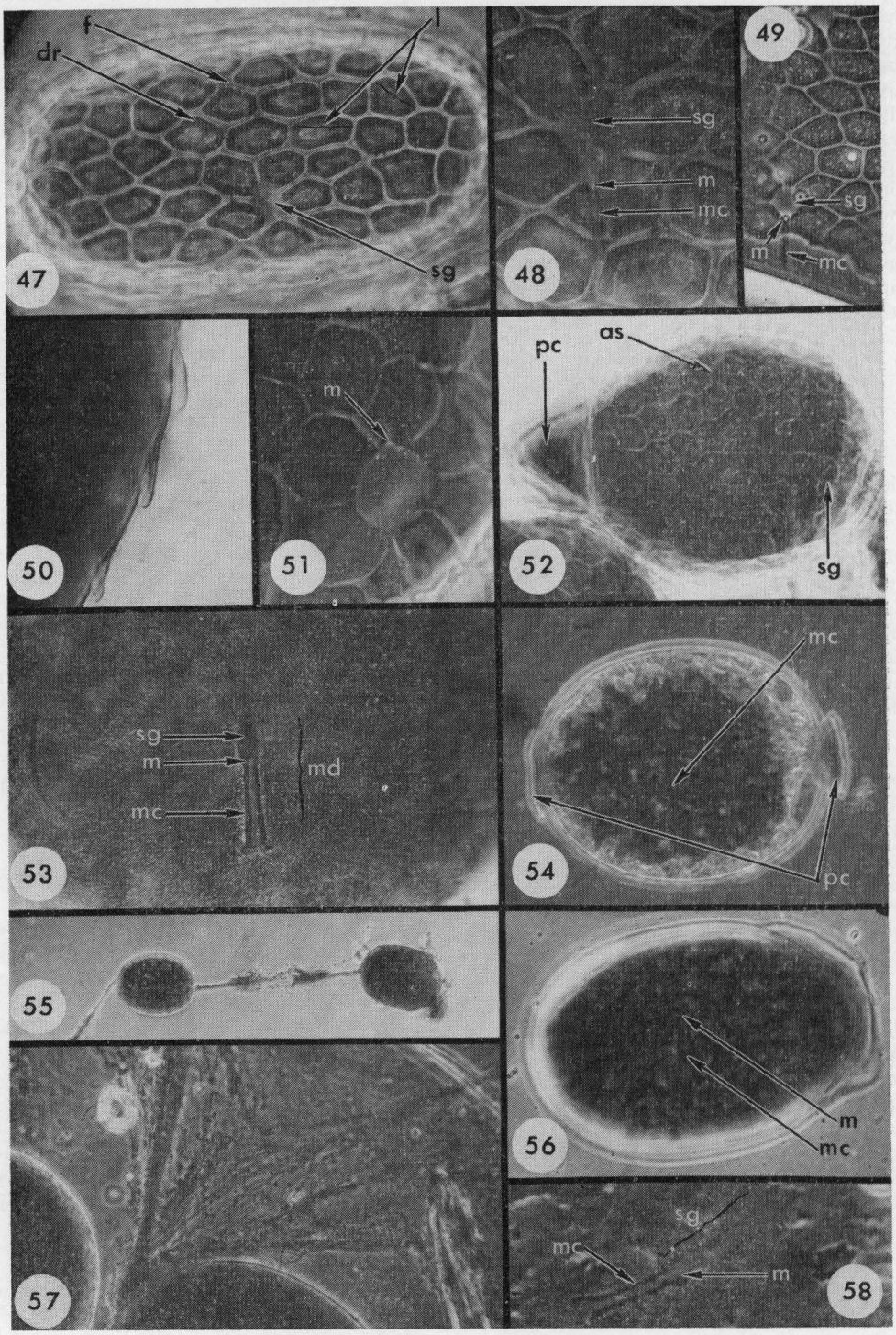

FIG. 47, 48.—*Ephemerella (E.) prudentalis.* 47, egg, laid in water, removed to 70% ETOH 12 hr later (375×). 48, same as Fig. 47, micropylar device (750×). FIG. 49.—*E. (E.) temporalis,* chorion and micropylar device (375×). FIG. 50–52.—*Tricorythodes atratus.* 50, tangential view (750×). 51, micropylar device (750×). 52, egg (300×). FIG. 53.—*Caenis jocosa,* micropylar device (750×). FIG. 54.—*C. forcipata,* egg (150×). FIG. 55.—*C. jocosa,* eggs with polar caps uncoiled (75×). FIG. 56.—*C. anceps,* egg (300×). FIG. 57, 58.—*C. forcipata.* 57, egg with threads of polar cap completely unraveled, laid in water, removed to 70% ETOH 12 hr later (300×). 58, micropylar device (750×).

varying from 15–31μ. The raised edges result in a large-mesh reticulation formed by furrows (spaces between the raised edges of the plates) 1.9–5.4μ wide, rather than ridges as stated by Smith (1935). When eggs are laid in water, the edges of these plates swell inwardly and upwardly to form suckerlike structures (Fig. 45), which undoubtedly serve, together with an adhesive layer, for the attachment of the egg. Many variously shaped granules and clear spots can be found on the suckerlike plates (Fig. 47–49).

The micropylar device is typical of the family (Fig. 47–49); sperm guide oval, 15–19μ long by 13–17μ wide; micropylar canal 23–38μ long.

The only character found to separate the eggs of *E. prudentalis* and *E. temporalis* is the presence of many clear spots on the plates of *E. temporalis* (Fig. 49), and the reduction or absence of these in *E. prudentalis* (Fig. 47, 48).

TRICORYTHIDAE

Genus *Tricorythodes* Ulmer

(Fig. 50–52)

Form.—Ovoid, with 1 polar cap which tapers to a nipplelike point.

Chorion.—Morgan (1913) described the egg of *T. allectus* (Needham) to be bright green with a yellowish cap and "with a prominent shingle-like surface." Smith (1935) disagreed with Morgan, believing the chorion to be "sculptured, not with 'shingles' as figured by Morgan (1913), but with a reticular pattern having the ridges interrupted in such a way that the egg appears to be covered with overlapping shingles or scales."

The surface of the egg actually does have a shinglelike surface (Fig. 50), and is not like the reticular pattern described and figured by Smith. These overlapping "shingles" or plates are mostly hexagonal and 15–19μ across. There is a curved band of small circular-mesh reticulation across the middle of each plate.

Attachment Structures.—In addition to the polar cap, there are a few pairs of relatively thick threads which are attached between the plates, and are not coiled (Fig. 52).

Micropylar Device.—Sperm guide oval, 15–23μ long by 13–17μ wide; micropylar canal difficult to see, but at least 9μ long; only 1/egg, and situated near the uncapped pole (Fig. 51, 52).

Characters could not be found to separate the eggs of *T. atratus, T. explicatus, T. fallax,* and *T. stygiatus.*

CAENIDAE

Genus *Caenis* Stephens

(Fig. 53–58)

Smith (1935) studied eggs of *C. amica* Hagen, *C. jocosa, C. hilaris* (Say), *C. perpusilla* Walker (from India), and *C. simulans;* and Degrange (1960) studied eggs of *C. horaria* (L.), *C. macrura* Stephens, *C. moesta* Bengtsson, *C. robusta* Eaton, and *Caenis* sp.

The 2 polar caps and the micropylar device are the 2 distinctive features of *Caenis* eggs. Most *Caenis* eggs have 2 polar caps; however, *Caenis* sp. described by Degrange, and *C. anceps* possess only 1. The polar caps, unlike the polar caps of other mayfly eggs, are composed of a mass of long, tightly cohering, spirally arranged threads with variously sized terminal knobs (Fig. 54–57) (according to Smith (1935) *C. perpusilla* has only 4 threads). Upon contact with water the threads uncoil (Fig. 55) and unspiral (Fig. 57), to become entangled with submerged surfaces (Fig. 57).

The micropylar device may lack the sperm guide and consist simply of an elongate micropylar canal (Fig. 56). However the distinctive feature is that the canal is the most evident part of the micropylar device (Fig. 53, 58). Unlike most other mayfly eggs, only 1 micropyle occurs on *Caenis* eggs except in *C. horaria,* where Degrange (1960) stated there are 2 present.

Smith (1935) observed a smooth chorion and 2 polar caps on the 5 species of *Caenis* eggs which he studied. I observed the eggs of 2 of these (*C. jocosa* and *C. simulans*) and found their chorion to be definitely sculptured.

KEY TO SPECIES

1. With 1 polar cap (Fig. 56); chorion mostly smooth, sculpturing absent except under the cap ..... ***anceps***
   With 2 polar caps (Fig. 54, 55); the entire chorion reticulate or finely punctate (Fig. 53, 58) 2
2. Chorion finely punctate, the punctures up to 0.5μ in diam (Fig. 58) ..... ***forcipata***
   Chorion finely reticulate with irregularly shaped polygonal mesh up to 1.2μ long (Fig. 53) .... ***jocosa***

Caenis anceps Traver

(Fig. 56)

Form.—Ovoid, with 1 polar cap.

Chorion.—Smooth, except for the area under the cap, which is coarsely and unevenly sculptured.

Attachment Structures.—The single polar cap is large, like *Caenis* sp. described by Degrange, and unlike the cap of other *Caenis* species, it encircles approximately one-fourth the egg.

Micropylar Device.—Sperm guide lacking; micropylar canal (23.1–29.2μ long) gradually expanding distally (3.1μ in outside diam at micropyle, 3.8–4.2μ in outside diam at distal end).

Caenis forcipata McDunnough

(Fig. 54, 57, 58)

Form.—Ovoid, with 2 polar caps.

Chorion.—Very finely punctate, the punctures approximately 0.5μ in diam (Fig. 58).

Attachment Structures.—Two polar caps.

Micropylar Device.—Sperm guide elongate, flame shaped, 15–30μ long; micropylar canal (22–27μ long, 3.1–3.8μ in outside diam at micropyle) mostly parallel sided, expanding suddenly at the distal end (5.4–6.9μ in outside diam) (Fig. 58). The expansion is a flaring, not a flange as in *C. jocosa* (Fig. 53).

Caenis jocosa McDunnough

(Fig. 53–55)

Form.—Ovoid, with 2 polar caps.

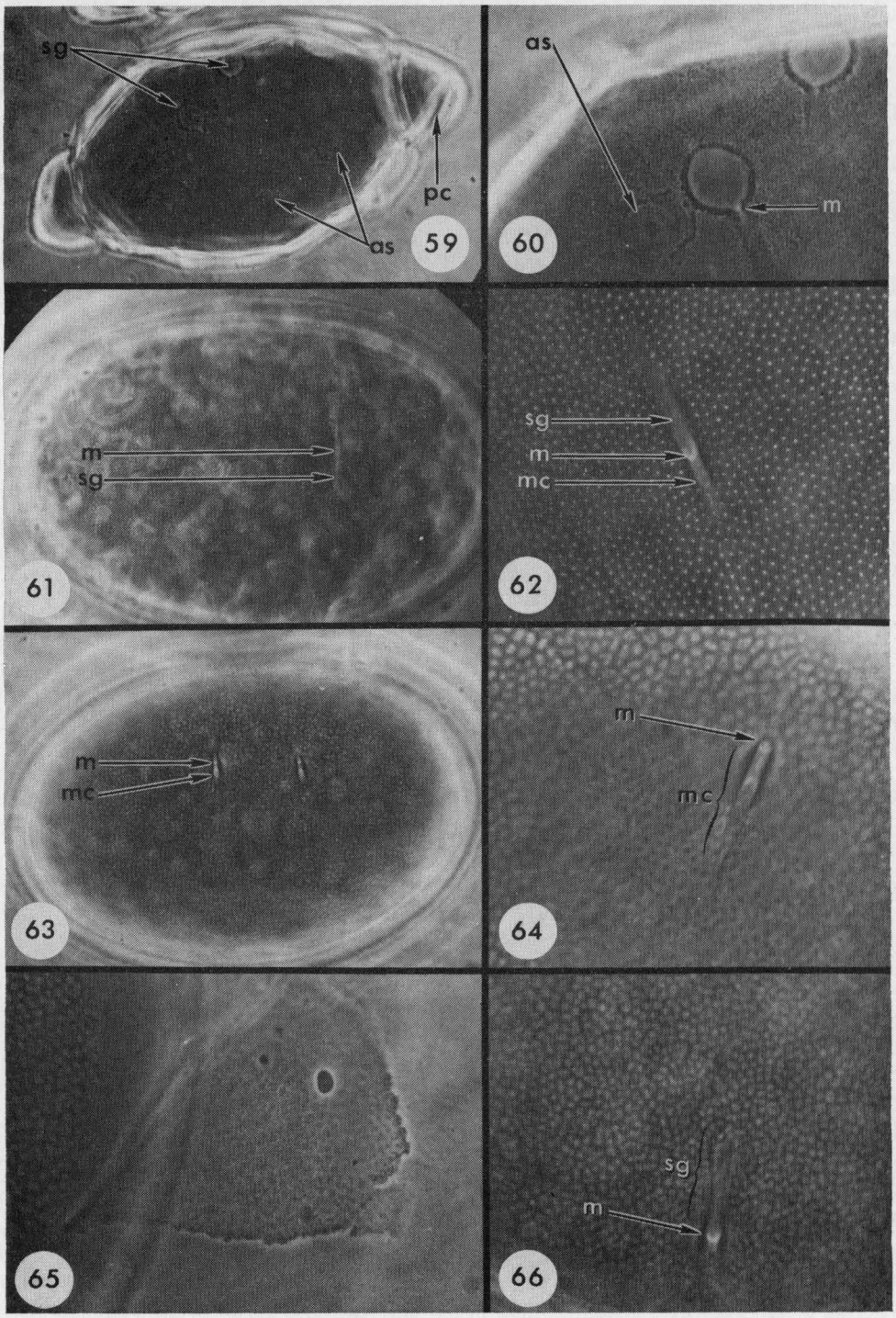

FIG. 59, 60.—*Potamanthus myops.* 59, egg (300×). 60, micropylar device (750×). FIG. 61, 62.—*Ephemera guttulata.* 61, egg (300×). 62, micropylar device (750×). FIG. 63–65.—*E. simulans.* 63, egg (300×). 64, micropylar canal (750×). 65, adhesive layer (750×). FIG. 66.—*E. varia,* micropylar device (750×).

Chorion.—Finely reticulated, the mesh measuring up to 1.2μ long (Fig. 53).

Attachment Structures.—Two polar caps.

Micropylar Device.—Sperm guide elongate, flame shaped, 8–22μ long; micropylar canal (15–24μ long, 2.3–3.1μ in outside diam at micropyle) parallel-sided or gradually expanding, often with an abrupt flange-like expansion at the distal end (4.6–6.9μ in outside diam.) (Fig. 53).

Caenis simulans McDunnough

C. simulans, as presently understood, can be broken into 3 separate groups based upon differences in the eggs. These are from Utah, from Michigan and New York, and from Michigan and Ontario. I am not yet prepared to say which one is (or that all are) the true *C. simulans.*

POTAMANTHIDAE

Genus *Potamanthus* Pictet

(Fig. 59, 60)

Ide (1935) and Smith (1935) examined eggs of *P. rufous* Argo, and Degrange (1960) examined those of *P. luteus* (L.).

Form.—Ovoid, with 2 polar caps. (Fig. 59, distorted by preservative).

Chorion.—Covered with many dark maculations (Fig. 60).

Attachment Structures.—Scattered about the surface are 6–12 coiled threads with terminal knobs (Fig. 59, 60, and similar to Fig. 40); the center of each knob is marked by a cluster of maculations. The coiled threads and the 2 polar caps are the only attachment structures. Ide's (1935) illustration of an egg of *P. rufous* shows the swelled caps which are characteristic of eggs laid in water.

Micropylar Device.—Sperm guide nearly circular, 11–23μ in diam; micropylar canal 4–15μ long. The sperm guide is clear of maculations, and is marked by a dark ring around its border. Usually 2, occasionally more, they are scattered in the equatorial region (Fig. 60).

Characters could not be found to separate the eggs of *P. myops* and *P. neglectus.*

EPHEMERIDAE

As in the Caenidae, the micropylar canal is the most evident part of the micropylar device on *Ephemera* and *Hexagenia* eggs. The sperm guide, when present, is somewhat variable but will serve to distinguish the 2 genera. The eggs are not equipped with accessory attachment structures or polar caps, their only method of attachment being an adhesive layer coating the eggs. Hunt (1951, 1953) relied on the adhesiveness of *Hexagenia limbata* (Serville) s. lat., eggs when he collected them with submerged glass plates. Eggs of *Pentagenia* were not studied.

KEY TO GENERA

Chorion with a large-mesh reticulation (mesh 13–31μ long) (Fig. 67–71); sperm guide always present as an elongate channel in the ridges of the reticulation (Fig. 67–71) ..... ***Hexagenia***

Chorion with a small-mesh reticulation (mesh 1.5–3.1μ long) (Fig. 63–66), or punctate (Fig. 61, 62); sperm guide, when present, simply an elongate depression devoid of sculpturing (Fig. 62, 66) ..... ***Ephemera***

Genus *Ephemera* Linnaeus

(Fig. 61–66)

Smith (1935) stated that the eggs of *E. blanda* Traver, *E. simulans,* and *E. varia* "are all plain ellipsoid . . . and they have no chorionic patterns or appendages. When they are laid in . . . water, the eggs scatter over the bottom but they are held together in small bunches by a more or less stringy gelatinous material."

Degrange (1960) stated that the exochorion of *E. danica* Müller and *E. vulgata* L., is very finely reticulated with an irregular polygonal mesh, and that the exochorion of *E. glaucops* Pictet is finely granulated. He mentioned the presence of an adhesive substance which is finely granular, and described a micropylar device which lacks a sperm guide, and in which the canal partially projects beyond the micropyle and above the surface of the chorion.

Two of the 3 species studied by Smith also were examined in the present study (*E. simulans* and *E. varia*). In both these species, and also in *E. guttulata,* the eggs have distinct chorionic sculpturings, and are ovoid in form. Eggs of *E. simulans,* when broken, best showed the finely granular adhesive substance observed by Degrange (Fig. 65). Eggs of *E. varia* that had been in water for 12 hr readily adhered to the glass vial in which they were laid, and displayed the same adhesive substance. However, here the granulations were not so closely spaced as in preserved material, for the adhesive layer swells when in water (and was probably also stretched when the eggs were removed from the vial).

Although the micropylar device is similar to that described by Degrange (1960), the micropylar canal is divided into 2 parts (Fig. 64): a proximal part with thick parallel walls, and a distal part with much thinner walls which taper inwardly from the proximal part (except in *E. guttulata*). In *E. simulans* and *E. varia,* the proximal part projects beyond the micropyle and above the surface of the chorion, and resembles a pincerlike structure (Fig. 63, 66). In *E. guttulata* and *E. varia* a sperm guide is present as an elongate depression devoid of sculpturing (Fig. 62, 66). Two or more micropyles may be present, and they are found scattered in the equatorial region of the egg.

KEY TO SPECIES

1. Chorion finely punctate (Fig. 61, 62) ..... ***guttulata***
   Chorion reticulate (Fig. 63, 66) 2
2. Micropylar device without a sperm guide (Fig. 63, 64) ..... ***simulans***
   Micropylar device with an elongate sperm guide (Fig. 66) ..... ***varia***

Ephemera guttulata Pictet

(Fig. 61, 62)

Chorion.—Very finely punctate, punctures less than 0.7μ in diam.

Micropylar Device.—Sperm guide elongate (19–30μ long), without definite boundaries; micropylar canal 26–54μ long (Fig. 62). The thick walls of the proximal part of the micropylar canal do not project above the chorion as in *E. simulans* and *E. varia,* and project only slightly beyond the micropyle; the distal portion of the canal tapers only slightly or not at all. Usually 1 micropylar device/egg, occasionally 2.

Ephemera simulans Walker

(Fig. 63–65)

Chorion.—Reticulated with a very small, irregular, polygonal mesh 1.5–3.1μ long (Fig. 63, 64). In preserved material the granular adhesive layer often appears to be the exochorion. However, eggs laid in water show that this granular layer is the adhesive layer, thus it is not to be confused with the reticulated exochorion (Fig. 65).

Micropylar Device.—Sperm guide lacking; micropylar canal 18–38μ long. Proximal part of micropylar canal (8–23μ long) with a very short section projecting beyond the micropyle and above the chorion, resembling a pincerlike structure; distal part of canal (10–15μ long) tapering inwardly from the proximal part (Fig. 63, 64).

Ephemera varia Eaton

(Fig. 66)

The eggs of this species resemble those of *E. simulans* except that the micropylar device is much longer (50–55μ long) because of the presence of a sperm guide.

Genus *Hexagenia* Walsh

(Fig. 67–71)

The chorionic sculpturing, the type of micropylar device, and the shape of the egg serve as diagnostic features to distinguish *Hexagenia* eggs from other Ephemeroptera eggs.

Smith (1935) studied eggs of 10 of the 14 species and subspecies of *Hexagenia* in North America, and found that all but *H. recurvata* Morgan (which is sparsely covered with small nodules) have a reticulation of large, irregular, polygonal mesh formed by ridges which may be either straight or sinuous. Smith stated that the ridges of *H. munda elegans* Traver, *H. limbata venusta,* and *H. rigida* are sinuous; those of *H. munda orlando* Traver and *H. munda marilandica* Traver vary (may be straight or sinuous or mixture of both); and the ridges of *H. atrocaudata* McDunnough, *H. bilineata* (Say), *H. limbata occulta, H. limbata viridescens* (Walker), *H. munda affiliata* McDunnough, and *H. munda elegans* Traver (as *H. weewa* Traver) are straight. My observations agree with those by Smith.

The sperm guide makes its way to the micropyle as an elongate channel in the ridges of the reticulation (Fig. 67–71); its proximal portion may vary in width from one species to another, and it may expand laterally as a depression in the chorion. The micropylar canal is the longest observed on any mayfly eggs, and together with the sperm guide its length may equal the width of the egg.

Hexagenia eggs are more nearly rectangular than most Ephemeroptera eggs.

Hunt (1951, 1953) recorded observations on the number of eggs produced, and found the number to be positively correlated with female body length. The total number of eggs varied between 2260 and 7684, and the body length varied between 19.9 mm and 30.3 mm. An average-sized female (24–25 mm) produced about 4000 eggs.

KEY TO SPECIES AND SUBSPECIES

1. Ridges of reticulation 2μ wide and strongly sinuous (Fig. 68); portion of sperm guide proximal to micropyle enlarged and oval, the width usually being at least 3 times the diameter of the micropyle (Fig. 68) ..... ***rigida***
   Ridges of reticulation 2–3.5μ wide, straight or only slightly sinuous (Fig. 67, 69–71); portion of sperm guide proximal to micropyle only slightly widened, not wider than twice the diameter of the micropyle (Fig. 69–71); of if the proximal portion of the sperm guide is enlarged and oval (Fig. 67), the width being at least 3 times the diameter of the micropyle, then the ridges are 3.5μ wide (Fig. 67) 2
2. Ridges of reticulation 3.5μ wide (Fig. 67); proximal portion of sperm guide enlarged and oval, the width usually being at least 3 times the diameter of the micropyle (Fig. 67) ..... ***munda munda***
   Ridges of reticulation 2μ wide, (Fig. 69–71); proximal portion of sperm guide only slightly widened, usually not wider than twice the diameter of the micropyle (Fig. 71) 3
3. Ridges of reticulation straight or very slightly sinous (Fig. 70, 71); micropylar canal usually longer than 67μ ..... ***limbata occulta***
   Ridges of reticulation definitely more strongly sinuous (Fig. 69); micropylar canal usually less than 67μ ..... ***limbata venusta***

Hexagenia limbata occulta (Walker)

(Fig. 70, 71)

Chorion.—Large-mesh (13–31μ long) reticulation formed by ridges (2μ wide) which are straight or only faintly hinting at sinuosity.

Micropylar Device.—Sperm guide 42–67μ long; micropylar canal 67–77μ long. The sperm guide gradually widens as it approaches the micropyle, but its width is typically not greater than twice the diameter of the micropyle (Fig. 70, 71).

Hexagenia limbata venusta Eaton

(Fig. 69)

Egg as in *H. l. occulta,* except the chorionic ridges are definitely sinous, although not so strongly as in *H. rigida;* and the micropylar canal is 44–67μ long.

Hexagenia munda munda Eaton

(Fig. 67)

Chorion.—Large mesh (13–31μ long) reticulation formed by straight or slightly sinuous ridges (3.5μ wide).

Micropylar Device.—Sperm guide elongate, 48–58μ long; micropylar canal 58–67μ long. The proximal portion of the sperm guide is an abruptly en-

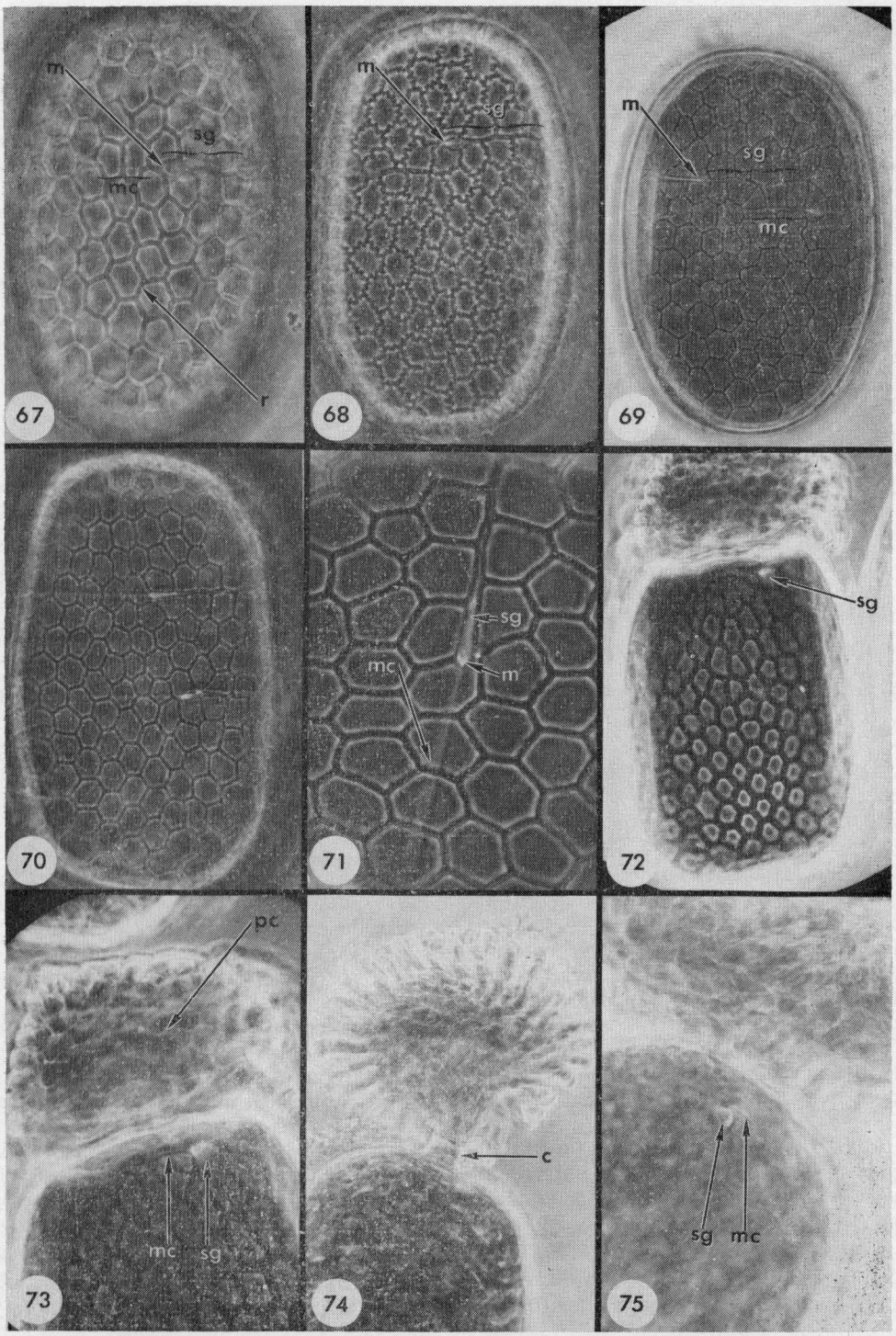

FIG. 67.—*Hexagenia munda munda*, egg (267×). FIG. 68.—*H. rigida*, egg (267×). FIG. 69.—*H. limbata venusta*, egg (267×). FIG. 70, 71.—*H. l. occulta*. 70, egg (267×). 71, micropylar device (667×). FIG. 72, 73.—*Ephoron leukon*. 72, egg (267×). 73, micropylar device (333×). FIG. 74, 75.—*E. album*. 74, collar surrounding base of polar cap (267×). 75, micropylar device (333×).

larged oval area, the width usually being at least 3 times as great as the diameter of the micropyle.

Hexagenia rigida McDunnough

(Fig. 68)

Chorion.—Large-mesh (13–31μ long) reticulation formed by ridges (2μ wide) which are strongly sinuous. A single tubercle is found nearly in the center of each mesh.

Micropylar Device.—Sperm guide elongate, 48–62μ long; micropylar canal 44–55μ long; the proximal portion of the sperm guide is an abruptly enlarged oval area, usually at least 3 times as wide as the diameter of the micropyle.

POLYMITARCIDAE

The eggs of the 2 subfamilies of Polymitarcidae have no characters in common, and the strong differences in their eggs suggest that they are not closely related. Only 1 subfamily has polar caps; and strikingly different micropylar devices, chorionic sculpturings, and methods of attachment can be noticed between the 2 subfamilies.

KEY TO GENERA

Eggs with a polar cap (Fig. 72–75); micropylar device with an oval-shaped sperm guide and an elongate micropylar canal (Fig. 72, 73, 75); "sides" nearly parallel ..... ***Ephoron***

Eggs without a polar cap (Fig. 76–79); micropylar device with a funnel-shaped sperm guide and a short micropylar canal (Fig. 77–79); egg with the appearance of a sphere which has had 1 side pushed in (Fig. 78) ..... ***Tortopus***

Genus *Ephoron* Williamson

(Fig. 72–75)

Smith (1935) studied what he thought to be *E. album* but actually looked at eggs of *E. leukon* as did Ide (1935). The egg of *E. virgo,* studied by Degrange (1960), is similar to that of *E. album* in that it lacks reticulation.

As many as 5 micropylar devices have been found at the capped end of the egg. The sperm guide is oval, and the micropylar canal is proximally expanded forming the "half-skullcap" described by Degrange (1956, 1960) for *E. virgo* (Fig. 72, 73, 75).

The only attachment structure is a large polar cap which is composed of many tubular-shaped structures (Fig. 72–75). Each of these structures, according to Degrange (1960), is composed of many threads with terminal knobs. This grouping of the threads into tubular-shaped structures is unique to *Ephoron.* The base of the cap is surrounded by a chorionic collar (Fig. 74), and this fact suggests that the cap is attached to the endochorion rather than the exochorion.

KEY TO SPECIES

Chorion smooth, without reticulation ..... ***album***

Chorion with a large-mesh (11–27μ long) reticulation (Fig. 72, 73) ..... ***leukon***

Ephoron album (Say)

(Fig. 74, 75)

Form.—Nearly rectangular, with 1 polar cap.

Chorion.—Smooth, sculpturing absent.

Micropylar Device.—Sperm guide oval, 7–10μ in diam; micropylar canal 13–21μ long. With the polar cap at "north" position, the sperm guide may be east or west of the micropylar canal (Fig. 75), whereas in *E. leukon,* the sperm guide is to the east of the canal (Fig. 73).

Ephoron leukon Williamson

(Fig. 72, 73)

E. leukon differs from *E. album* by the possession of a chorionic reticulation of large, irregular, polygonal (mostly hexagonal) mesh formed by ridges 3–8μ wide. The length of the mesh ranges from 11 to 27μ.

Genus *Tortopus* Needham & Murphy

(Fig. 76–81)

Two collections of females, each from different localities, appear to be different species, and this hypothesis is supported by the eggs. Since they cannot be named they will be designated by numbers and place collected.

KEY TO SPECIES

Chorionic punctures large, 3–6μ in diam (Fig. 76, 77, 79); adhesive layer composed of threads radiating from many small circular areas (Fig. 80); threads terminated by knobs with no particular pattern of arrangement ..... ***Tortopus*** sp. no. 1. Alabama

Chorionic punctures small, less than 1.2μ in diam; adhesive layer composed of a maze of threads, which lack any pattern of arrangement; threads bear knobs arranged in a "floral" pattern (Fig. 81) ..... ***Tortopus*** sp. no. 2. Texas

Tortopus sp. no. 1. Alabama

(Fig. 76–80)

Form.—The egg has the appearance of a sphere which has had 1 side pushed in (Fig. 78). Smith (1935) observed that the shape probably aided storage of the eggs in the female's abdomen.

Chorion.—Very evenly punctate with large, widely spaced circular punctures 3–6μ in diam (Fig. 76, 77, 79).

Attachment Structures.—The egg is covered by an adhesive layer which, under 1250 magnifications, is readily seen to be composed of a dense mat of threads (Fig. 76), many of which are terminated by knobs. In most areas the threads are so numerous and intermingled that it is impossible to discern their terminus or point of attachment. However, in those areas where the threads are not so numerous, the attachment of the threads can be found to be as shown in Fig. 80. These threads radiate from a central area which has no definite border. Some of the radiating threads connect to other thread-radiating areas, and some are lost to the maze of threads with terminal knobs. It appears that the radiating areas are columns composed of threads perpendicular to the chorion and attached in the chorionic punctures; this is hypothesis, however, for nothing could be definitely decided about the actual nature of attachment of the threads to the chorion.

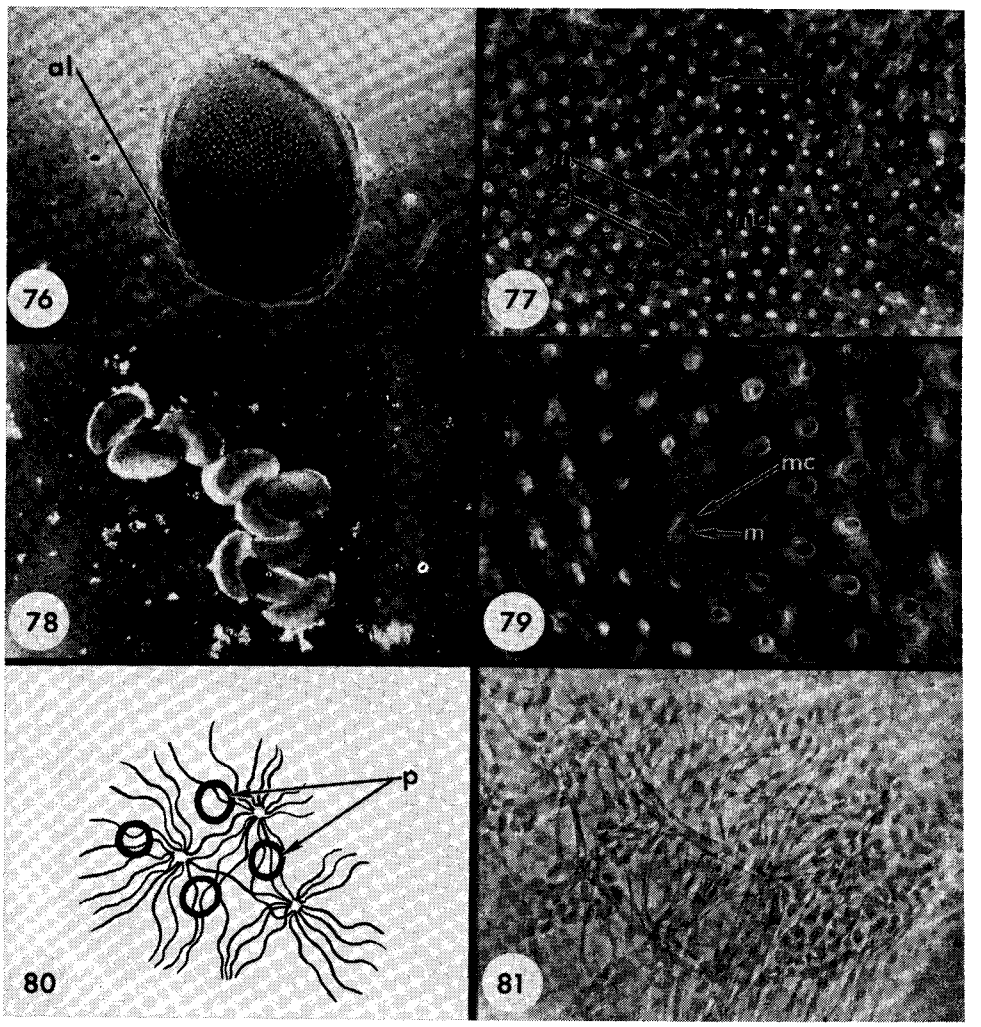

FIG. 76–80.—*Tortopus* sp. no. 1. Alabama. 76, egg (94×). 77, micropylar device (300×). 78, stacked eggs (34×). 79, micropylar device (750×). 80, diagrammatic view of threads composing the adhesive layer (viewed at 1250×). FIG. 81.—*Tortopus* sp. no. 2. Texas, adhesive layer (938×).

Micropylar Device.—Sperm guide funnel shaped, rim 28–40μ in diam (Fig. 77); the ovoid micropyle is followed by a short micropylar canal 3–10μ long (Fig. 79). Only 1 micropyle present/egg.

Tortopus sp. no. 2. Texas

(Fig. 81)

Differs from *Tortopus* sp. no. 1 in features of the chorion and attachment structures.

Chorion.—Very evenly punctate with small, widely spaced circular punctures less than 1.2μ in diam.

Attachment Structures.—The thread-radiating areas as in sp. no. 1 could not be found. However, there is a peculiar arrangement of the terminal knobs—many terminal knobs are grouped in a "floral" arrangement (Fig. 81), rather than being independent of one another as in sp. no. 1.

SUMMARY

The morphological features found on Ephemeroptera eggs have been shown to aid the taxonomy of adult and nymphal females. A simple technique for preparing the eggs permitted a detailed morphological study. The structural modifications on the eggs have allowed significant contributions to the taxonomy of Heptageniidae at the generic level; to *Ephemerella* at the subgeneric level (separation of the subgenus *Eurylophella* from the other subgenera of *Ephemerella*); and to Leptophlebiidae, Caenidae, *Hexagenia* (Ephemeridae), and Polymitarcidae at the specific level.

The eggs of Heptageniidae, Leptophlebiidae, Caenidae, *Hexagenia* and *Tortopus* (Polymitarcidae) are apparently diverse enough at the specific level to warrant further study. On the other hand, the eggs of Ephemerellidae, Tricorythidae, and Potamanthidae are not diverse enough to allow specific-level determinations. It is also doubtful that many of the subgenera of *Ephemerella* can be distinguished by the eggs. Sufficient study has not yet been done on the eggs of Siphlonuridae and Ametropodidae to assess their contribution to taxonomy.

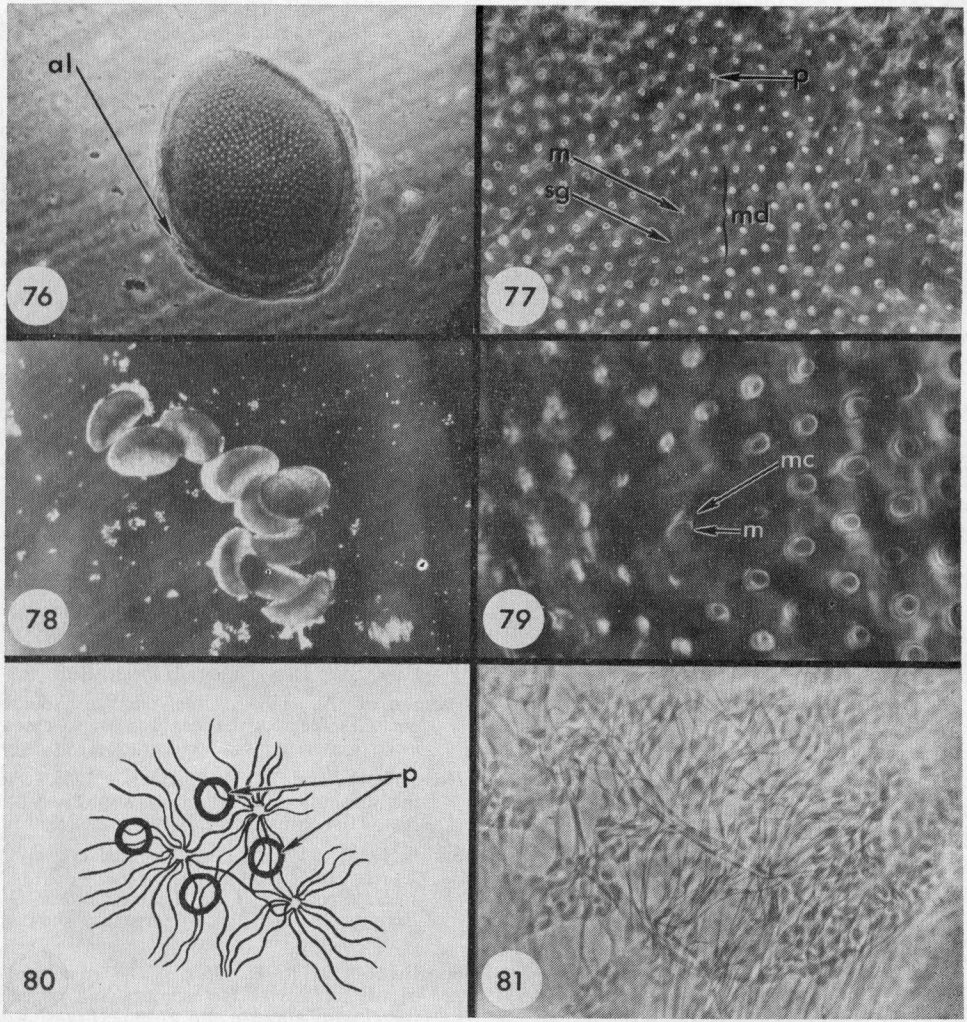

FIG. 76–80.—*Tortopus* sp. no. 1. Alabama. 76, egg (94×). 77, micropylar device (300×). 78, stacked eggs (34×). 79, micropylar device (750×). 80, diagrammatic view of threads composing the adhesive layer (viewed at 1250×). FIG. 81.—*Tortopus* sp. no. 2. Texas, adhesive layer (938×).

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